

# A taxonomic revision of the genus *Oedaleus* Fieber (Orthoptera: Acrididae)

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## Synopsis

The economically important grasshopper genus *Oedaleus* is revised. Twenty species and three subspecies are described, keyed and illustrated. *O. nadiæ*, *O. plenus browni* and the male of *O. miniatus* are described as new to science. Four species and five subspecies are synonymized and two species are reduced to subspecies, one being transferred from the genus *Gastrimargus*. All available primary types have been examined and four neotypes have been designated. Five lectotypes for senior synonyms and seven for junior synonyms have been designated. The biology and economic importance of the species are reviewed and their distributions are mapped. The biogeography of the genus is discussed in the light of past and present geological, vegetational and climatic factors. The fluctuations of the equatorial *Brachystegia* woodland zone in Africa during the Pleistocene are advanced as an explanation of the observed trans-equatorial speciation in *Oedaleus* and some other dry savannah organisms.

## Introduction

In recent years members of the genus *Oedaleus* have increasingly been designated as crop pests in Africa, India and South East Asia. The most serious damage has been caused by *Oedaleus*

*senegalensis*, a widespread and economically important species, reviewed by Batten (1969). The growing list of described species, and their possible economic importance, have highlighted the lack of any comparative taxonomic and biogeographical study and the need for accurate identification and a more certain knowledge of relationships within the genus. Descamps (1972), speaking at the International Study Conference on the Current and Future Problems of Acridology, included *Oedaleus* among a short-list of genera urgently in need of revision.

This study is intended to facilitate accurate identification of all *Oedaleus* species by agriculturists, ecologists and entomologists involved in locust control and crop protection. To guarantee stable nomenclature, all available primary types have been examined, and neotypes have been designated to replace lost types. In cases where a holotype was not originally designated, lectotypes have been selected from the syntype series. Keys to, and descriptions of all the species and subspecies are included, with figures to illustrate the more important morphological characters. Accurate distribution maps have been compiled, based largely upon data from the labels of the many thousands of specimens examined. Supplementary data have been obtained from correspondents and from reliable published sources. The biogeography of the genus is discussed in the light of known past and present geological, vegetational and climatic features, and the available information on the life histories, biology and economic importance is assembled.

### History of the genus *Oedaleus*

The genus *Oedaleus* was erected as a subgenus of *Oedipoda* by Fieber (1853) to accommodate *Acrydium nigrofasciatum* De Geer, 1773. Stal (1873) made *Oedaleus* a subgenus of *Pachytylus* Fieber, 1853 and added to it three species now included in *Gastrimargus*, as well as *Gryllus Locusta flavus* Linnaeus, 1758 and *Gryllus abruptus* Thunberg, 1815. He also synonymized *Gryllus arcuatus* Thunberg, 1824 with *Oedaleus nigrofasciatus* (De Geer, 1773), a fact overlooked by both Kirby (1910) and Johnston (1956).

Saussure (1884) gave *Oedaleus* full generic status and divided it into two subgenera, *Oedaleus* s. str., and the newly-erected *Gastrimargus*. He described *Oedaleus infernalis* and transferred *Pachytylus senegalensis* Krauss, 1877, but placed *Oedaleus flavus* (Linnaeus, 1758) in the genus *Humbella*. Unfortunately, he later (Saussure, 1888) described the same insect as *Oedaleus nigrofasciatus* var. *citrinus* and, despite the use of the older name by Karsch (1887) and Kirby (1902a), Saussure's name remained in common use as *Oedaleus citrinus* Saussure (Distant, 1892) until the synonymy was revealed by Dirsh (1961a). Linnaeus (1758) assumed that his *Gryllus Locusta flavus* was identical with the '*Locusta capensis alis inferioribus luteis*' described by Petiver (1702) but in the absence of surviving material Petiver's figure cannot definitely be proved to represent this species. *Gryllus Locusta flavus* was wrongly identified with *Acrydium nigrofasciatum* De Geer, 1773, by De Geer himself and by several subsequent authors, although Kirby (1910) pointed out that the *Gryllus flavus* of Fabricius, 1775, a junior synonym of *Oedaleus nigrofasciatus*, should not be considered identical with the *G. L. flavus* of Linnaeus, known to Kirby as *Humbe flava*. He was also aware that the *G. L. flavus* of Stoll (1813) was not the same species as that of Linnaeus, and synonymized it (incorrectly) with *Oedaleus arcuatus* (Thunberg, 1824), which was itself a synonym of *Oedaleus nigrofasciatus* unbeknown to him.

This situation was further complicated by the fact that *Oedaleus nigrofasciatus*, a purely South African species, was always confused with the Mediterranean *Oedaleus decorus* (Germar, 1826), the older name being used indiscriminately until Uvarov (1923) finally demonstrated the separate identity of the two species. Since then some confusion of *O. decorus* and *O. nigrofasciatus* has continued (Hollande, 1926; Jovančić, 1953; Barbut, 1954; Rungs, 1962). *Oedaleus australis* Saussure, 1888, originally described as *O. nigrofasciatus* var. *australis* and given specific status by Kirby (1910), has also been the subject of some confusion. It was frequently identified as *O. senegalensis* (Krauss, 1877) (Froggatt, 1903; 1907; 1910; Sjöstedt, 1920; 1921; Zacher, 1925; 1949), although Uvarov (1930a) gave reasons for believing the Australian species to be distinct from the African one.

Kirby (1910) synonymized *Ctyphippus arenivolans* Butler, 1881 and *Pachytylus mlodziwiztcki*



Bolivar, 1887 with *O. senegalensis*. Distant (1892) transferred *Epacromia plena* Walker, 1870 to *Oedalus* [sic], and Uvarov (1925) synonymized *O. nigrofasciatus* var. *caffer* Saussure, 1888 with this species and transferred *Chortoicetes interruptus* Kirby, 1902 to *Oedaleus*. Throughout the last century numerous new species and subspecies have been described, notably by Uvarov (six species), but there has not been any revisionary treatment of the genus and nomenclatural changes have been limited to those outlined above.

At the commencement of the present study 24 species and four subspecific taxa were recognized.

### Materials, methods and terminology

Measurements used in this study generally follow Dirsh (1953) except that total length is here defined as the distance from the frons to the apices of the folded tegmina, as used by Jago (1963), not to the end of the abdomen as used by Dirsh and several other authors; head width is here measured across the genae (Dirsh, 1953) or across the eyes (Jago, 1963), whichever is the larger. The forewing is referred to as the tegmen, not the elytron. All measurements are given in millimetres and were made with Mauser dial calipers graduated with 0.05 mm divisions.

The male genitalia figured in this study were removed and treated in the manner described by Dirsh (1956*b*). Female spermathecae were examined by removal of the posterior abdominal segments and maceration in 10% potassium hydroxide solution. The abdomen was then slit open along the lateral intersegmental membrane to display the spermatheca. After examination genitalia preparations were placed in 70% alcohol with a little glycerine, contained in a polythene vial with a silicone rubber stopper pinned to the appropriate insect specimen.

Abbreviations of terms used in the descriptions and figures of the male genitalia are as follows: A – ancorae of epiphallus; Ac – arch of cingulum; Ap – anterior projections of epiphallus; Apv – apical valves of penis; Apd – apodemes of cingulum; B – bridge of epiphallus; Bp – basal valves of penis; Cv – cingular valves; Dp – dorsal process of cingulum; Ejd – ejaculatory duct; E – ejaculatory sac; Gpr – gonopore process; L – lophi of epiphallus; Lp – lateral plate of epiphallus; Pp – posterior projections of epiphallus; Rm – rami of cingulum; Sps – spermatophore sac. These and most other morphological terms relating to acridids are described and illustrated by Dirsh (1965). Since the genitalia of all species are very similar only those of *O. senegalensis* (Figs 60–64) have been labelled.

The nomenclature of the female spermatheca used in this study is that of Dirsh (1957). The term 'apical diverticulum' is thus understood to denote the bulbous blind-ending sac at the distal extremity of the spermathecal duct. In *Oedaleus* and other Acrididae this may be simple or it may possess a secondary diverticulum, which is usually much smaller. The apical diverticulum is always strongly recurved at its proximal end, and always continues in the direction of the coiling of the duct. The secondary or preapical diverticulum, on the other hand, when not reduced to a mere vestige, projects from the main duct at right angles on the outside of the coil. Since the secondary diverticulum is always smaller than the main seminal reservoir and is often absent, it is reasonable to refer to it as 'preapical' and to the larger diverticulum as 'apical'. However, Slifer (1939), a pioneer of the comparative study of the spermatheca, and other authors have used exactly the opposite designations, thus introducing some confusion. Recently Amedegnato (1976) has confirmed the nomenclature of Dirsh, used here, on the grounds that in the primitive condition there is only one diverticulum which should therefore be called apical.

The terminology of the venation used here is that of Ragge (1955). Except where otherwise stated, material examined is from the collections of the British Museum (Natural History), London.

To save space the label data for material examined of the commoner species have been abbreviated to country and locality only, excepting data for type-material which are given in full. For *O. senegalensis* and *O. decorus decorus* only countries are listed. A full list of all the material of *Oedaleus* species examined during the course of the study has been deposited in the British Museum (Natural History) and the Centre for Overseas Pest Research.

Distances and altitudes are given in SI units whatever the units of the original source.

## Depositories

MA, Addis Ababa	Ministry of Agriculture, Addis Ababa.
MNHU, Berlin	Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin.
ANIC, Canberra	Australian National Insect Collection, Canberra.
MHN, Geneva	Muséum d'Histoire Naturelle, Geneva.
MCSN, Genoa	Museo Civico di Storia Naturale, Genoa.
BPBM, Honolulu	Bernice P. Bishop Museum, Honolulu.
ZI, Leningrad	Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad.
MLZA, Lisbon	Museu e Laboratório Zoológico e Antropológico, Universidade de Lisboa, Lisbon.
BMNH	British Museum (Natural History), London.
COPR, London	Centre for Overseas Pest Research, London.
UM, Oxford	Hope Entomological Collections, University Museum, Oxford.
MNHN, Paris	Muséum National d'Histoire Naturelle, Paris.
ANS, Philadelphia	Academy of Natural Sciences, Philadelphia.
DATS, Pretoria	Department of Agricultural Technical Services, Pretoria.
CAS, San Francisco	California Academy of Sciences, San Francisco.
NR, Stockholm	Naturhistoriska Riksmuseum, Stockholm.
ZIUU, Uppsala	Zoologiska Institutionen, Uppsala Universitet, Uppsala.
NM, Vienna	Naturhistorisches Museum, Vienna.
USNM, Washington	United States National Museum, Washington.

## *OEDALEUS* Fieber

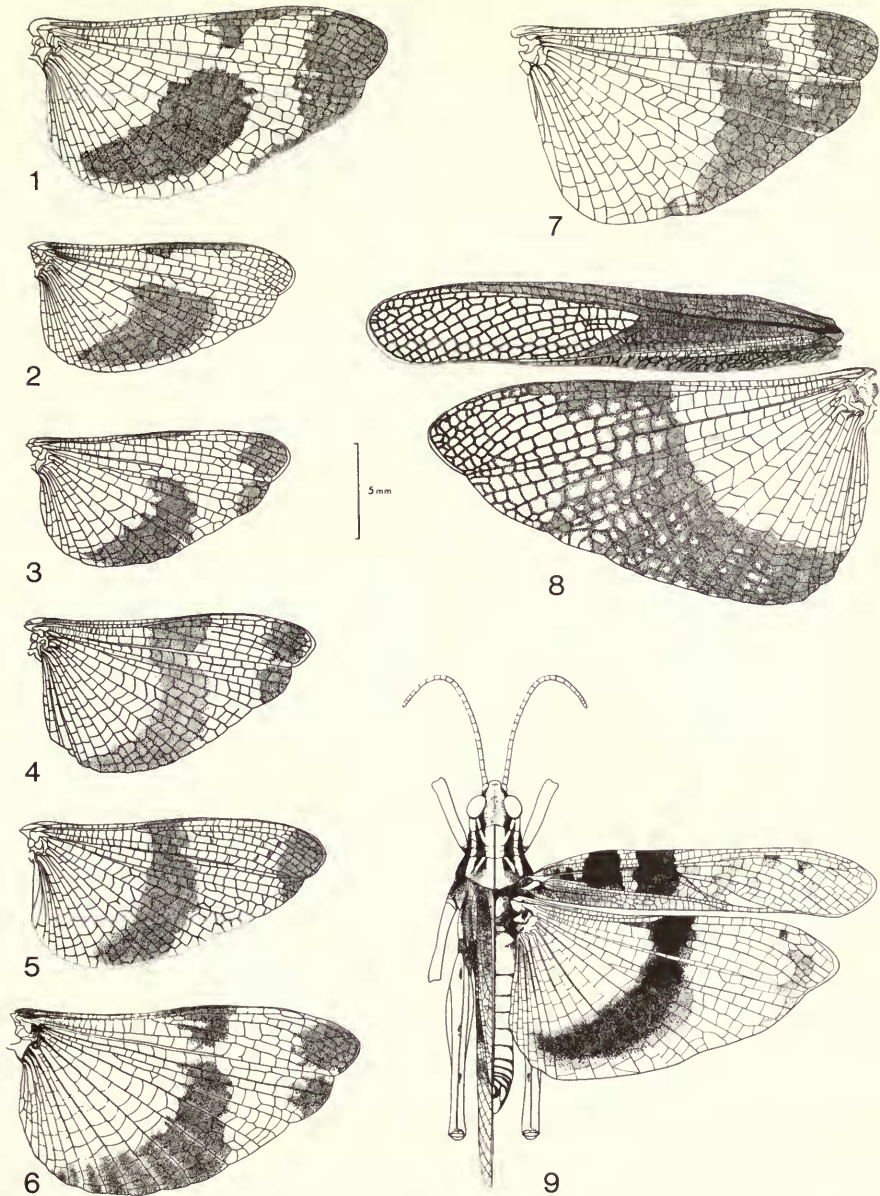
*Oedaleus* Fieber, 1853: 126 [as subgenus of *Oedipoda* Serville]. Type-species: *Acrydium nigrofasciatum* Degeer, 1773, by monotypy.

*Oedaleus* Fieber; Stål, 1873: 123 [as subgenus of *Pachytylus* Fieber].

*Oedaleus* Fieber; Saussure, 1884: 50.

Medium size (total length: 20–44 mm in male, 25–49 mm in female). Integument rugose and pitted. Fastigium of vertex angular with truncate apex, flat or slightly concave, with obtuse lateral carinulae variable in emphasis, with or without median longitudinal carinula; fastigial foveolae obsolete. Antennae (except in *O. miniatus*) filiform, as long as, or longer than length of head and pronotum together. Frons in profile oblique, convex, straight, or concave; frontal ridge sulcate with marginal carinulae diverging ventrally, reaching or not reaching clypeus. Eyes elongate-oval to oval, long axis vertical. Pronotum from high tectiform to saddle-shaped, constricted anterior to and at junction of prozona and metazona, wider and with distinct 'shoulders' in metazona; median carina linear, often intersected by posterior transverse sulcus; raised lateral carinae absent in most species, occasionally present in prozona underlying anterior arms of X-marking; metazona equal to or little longer than prozona, rarely (in *O. interruptus*) much longer, posterior margin rounded or angular; mesosternal interspace wider than long, widening posteriorly, usually wider than metasternal interspace. Tegmina and wings fully developed, or only slightly abbreviated; intercalary vein of medial area of tegmen well developed and finely serrate, at least in males, continuing to distal apex of medial area; membrane of tegmen semi-transparent with variable reticulation in basal half. Hind femur slender or broad, exterior ventral knee lobe acutely rounded; hind tibia as long as femur, apical spurs not specialized; arolium of medium size or small. Male supra-anal plate shield-shaped, rounded triangular; cercus conical, apically acutely rounded, of variable length; subgenital plate (except in *O. miniatus*) short, subconical with rounded apex; epiphallus bridge-shaped with well-developed ancorae and large, bilobate lophi; ectophallic membrane sclerotized and forming sheath below apical penis valves; cingulum with horseshoe-shaped arch bearing moderately long apodemes; cingular valves acute, less sclerotized than apical penis valves; basal penis valves with anterior lateral expansions, sometimes recurved, flexure narrow; apical penis valves short, acute, with serrated ventral subapical process. Female ovipositor short, valves robust, vertically excurved; spermatheca with sac-like apical diverticulum with or without a short preapical diverticulum.

General coloration variable, greenish or brownish with contrasting light and dark markings. Genae of head with oblique light and dark markings. Pronotum with variable dorsal light markings in the form of an X, lacking central intersection and divided into four arms by median carina and posterior transverse sulcus. Anterior arms of X often continued anteriorly onto head, crossing or not crossing eyes as a pale longitudinal stripe. Lateral lobes of pronotum with distinct white oblique marking centrally, sometimes reaching hind margin. Tegmina and hind femora with corresponding transverse light and dark bands, variable, sometimes obscure. Hind wing weakly or strongly tinted with yellow, pink, or red, usually but not always bounded by a dark fascia; remainder



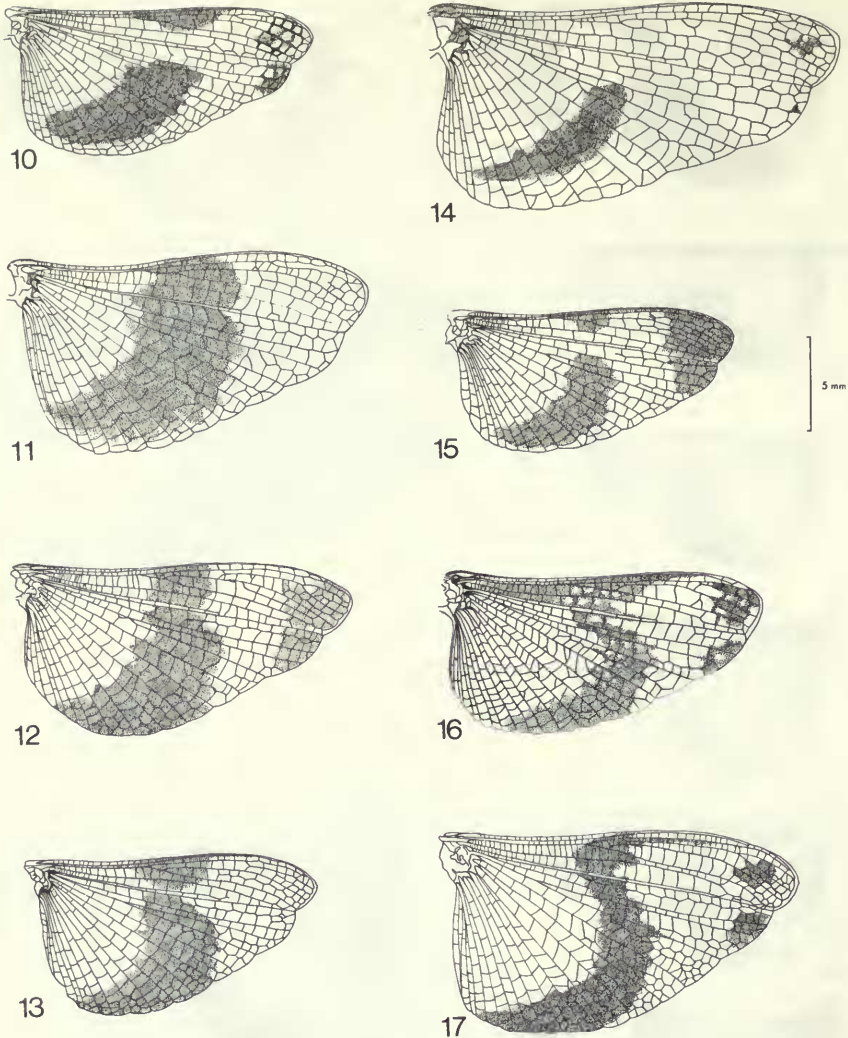
Figs 1–9 *Oedaleus* species (males), wings 1, *O. australis*; 2, *O. abruptus*; 3, *O. obtusangulus*; 4, *O. rosescens*; 5, *O. infernalis*; 6, *O. plenus plenus*; 7, *O. formosanus*; 8, *O. senegalensis* (melanic); 9, *O. senegalensis* (normal).

of wing transparent, colourless, sometimes apically darkened. Interior surface of hind femur straw-coloured, red, or mauve; tibiae red, straw-coloured, or grey.

#### Taxonomic affinities and diagnostic characters

*Oedaleus* falls naturally within the subfamily Oedipodinae, recently reinstated by Dirsh (1975). It comprises a homogeneous group of species found widely in the Old World tropics and subtropics. It may be distinguished from related genera by a combination of the following characters: the presence of a wing band in most species, the form and markings of the pronotum, the hind femur having the



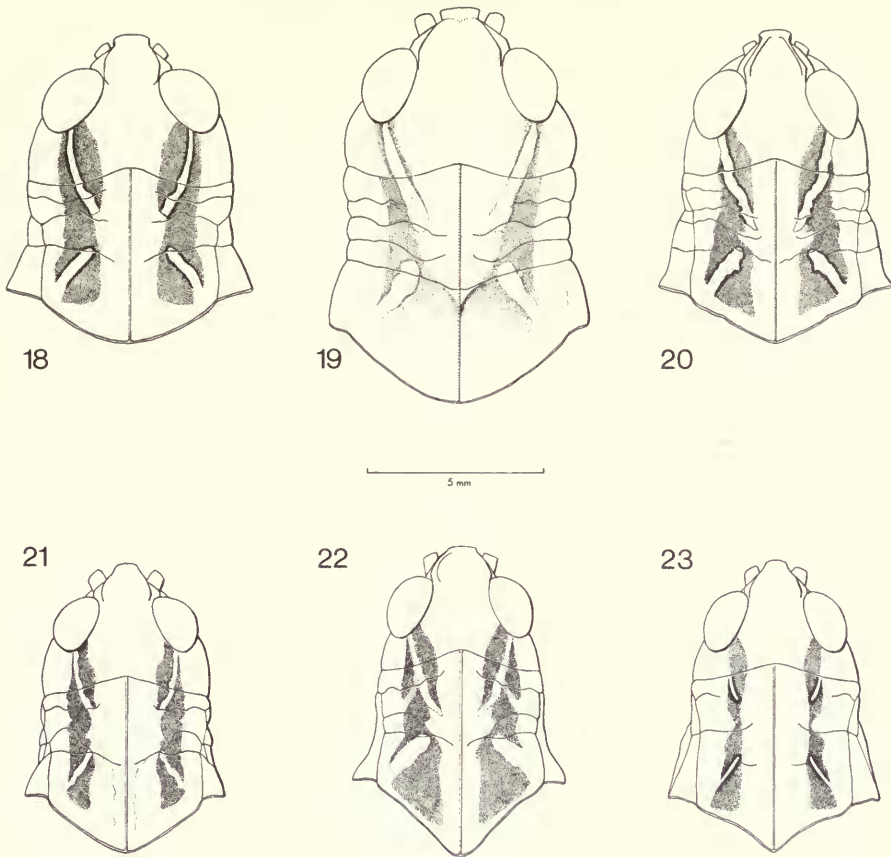


Figs 10–17 *Oedaleus* species (males), wings. 10, *O. nigriensis*; 11, *O. decorus decorus*; 12, *O. instillatus*; 13, *O. interruptus*; 14, *O. johnstoni*; 15, *O. carvalhoi*; 16, *O. miniatus*; 17, *O. flavus*.

upper marginal area not excised and lower marginal area not expanded, the tegmen lacking specialized stridulatory veinlets and by the short apical penis valves. It may be distinguished from the closely related genus *Gastrimargus* Saussure by the following key.

- |   |   |                     |
|---|---|---------------------|
| 1 | Pronotal X-marking with anterior and posterior arms continuous; posterior arms usually curved and with slightly convergent apices. Hind margin of pronotum rectangular to acutangular, never rounded  | <b>GASTRIMARGUS</b> |
| – | Pronotal X-marking always with anterior and posterior arms separate; posterior arms straight, not converging. Hind margin of pronotum rounded to rectangular, never (except in <i>O. interruptus</i> , <i>O. miniatus</i> , and some <i>O. plenus</i> ) acutangular | <b>OEDALEUS</b>     |

As indicated by the rather poor characters given above, there are no reliable objective criteria for separating the genera *Oedaleus* and *Gastrimargus* in their entirety one from the other. However, all the species presently considered as members of either of these genera are more closely allied to their congeners than to any member of the other genus. Saussure (1884) separated out *Gastrimargus* as a



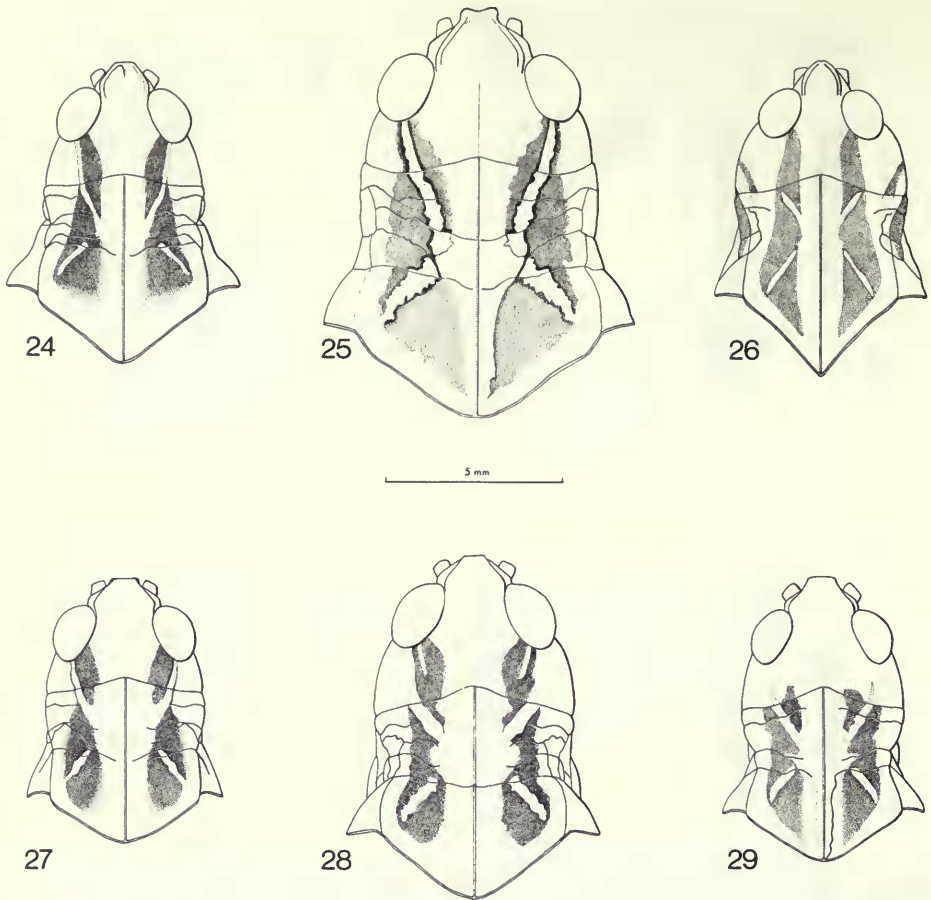
**Figs 18–23** *Oedaleus* species (females), heads and pronota, dorsal view. 18, *O. senegalensis*; 19, *O. johnstoni*; 20, *O. nigriensis*; 21, *O. nigrofasciatus*; 22, *O. plenus* (brown form); 23, *O. carvalhoi* (green form).

subgenus of *Oedaleus* largely on the basis of an overall impression of stoutness in the former. *Gastrimargus* later rose to generic status without any reasoned defence of its elevation (Kirby, 1910).

Saussure himself and later authors have sometimes experienced difficulty in referring marginal species to one genus or the other.

It is probable (but not yet certain) that all or most species of *Oedaleus* possess a pronotal repugnatorial gland and that, by contrast, *Gastrimargus* species do not. This may in the future give a more certain separation between the two genera. At present the division is workable and convenient since it enables the separation of 40 or so species into two almost equal groups of species with distinct ecological preferences. It appears that *Oedaleus* species are basically characteristic of sub-desert steppes and dry grasslands while *Gastrimargus* species are found in more humid wooded savannahs and tall grass.

Despite the uniformity of morphology within the genus, useful characters for species identification can be obtained by close examination. These include the shape and patterning of the dorsal surface of the pronotum (Figs 18–38), the banding or lack of banding on the hind wing (Figs 1–17), and the coloration of the ventral surface of the hind femora. The male genitalia offer some useful supporting characters which may, however, be difficult to interpret. In the females some additional information can be gained by studying the ventral surface of the ovipositor valves (Figs 39–59). However, the spermatheca is of little value for identification, being variable within one species and rather uniform within the genus as a whole.



Figs 24–29 *Oedaleus* species (females), heads and pronota, dorsal view. 24, *O. virgula* (brown form); 25, *O. inornatus*; 26, *O. interruptus*; 27, *O. australis*; 28, *O. decorus decorus* (green form); 29, *O. decorus asiaticus* (brown form).

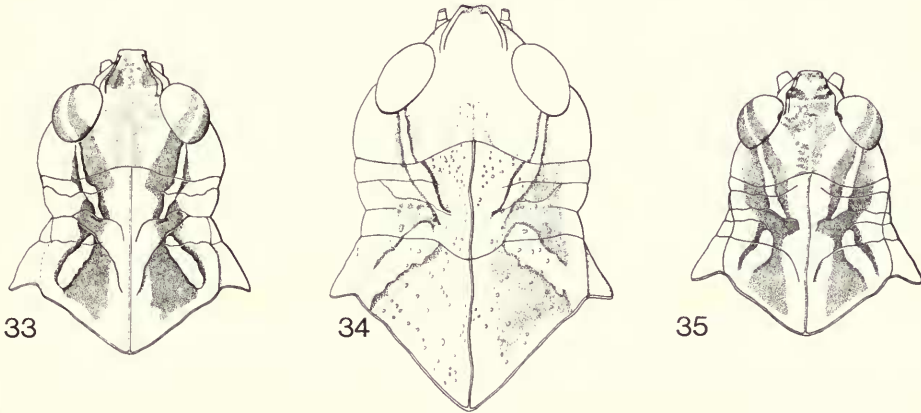
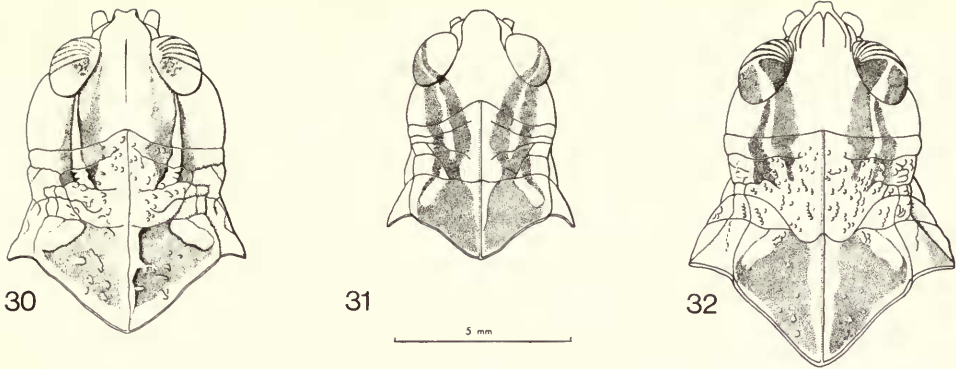
#### Keys to the species of *Oedaleus*

These are the first keys designed to facilitate the identification of all the known species of the genus *Oedaleus*. Keys to *Oedaleus* species occurring in eastern Asia were published by Chang (1939) and by Bei-Bienko & Mishchenko (1951*b*) but these are of little value since insufficient attention was paid to the examination of type-material and assessment of the range of infra-subspecific variation. Succeeding students of the subject have uncritically adopted the erroneous judgements of earlier authors with the result that the keys presently in use serve merely to distinguish imaginary taxa by the use of thoroughly unreliable characters. Thus the subspecies *O. infernalis pendulus* Steinmann (1965) was distinguished from other supposed subspecies largely on the basis of the proportions of the medial antennal segments. I am indebted to L. L. Mishchenko (pers. comm.), who has seen the type, for the information that it is in fact a junior synonym of *Dociostaurus maroccanus* (Thunberg).

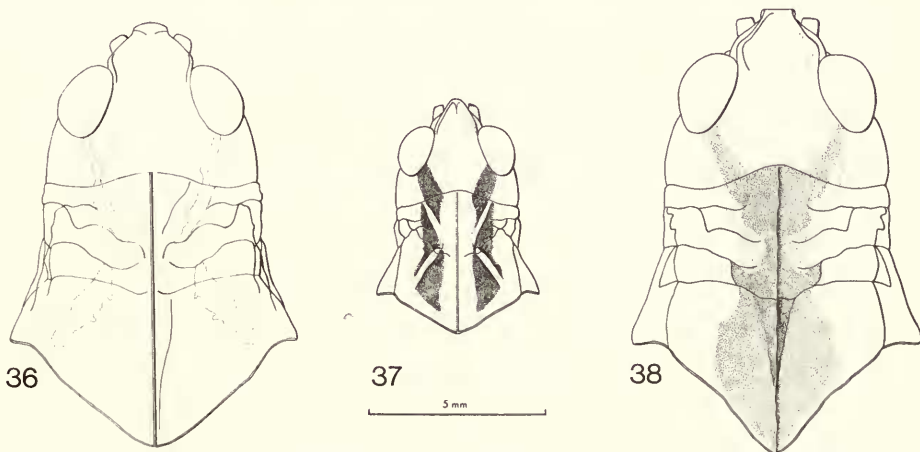
For brevity and ease of use, two keys are here provided, one covering Africa and its islands, Arabia and Madagascar, and the other dealing with the rest of the old world. In this way a specimen from Asia can be identified without needing to compare it with more than a dozen species which are known to be restricted to the Ethiopian Region. Some widespread species occur in both keys, and variable species are keyed out twice in the same key.

As in some other recent generic revisions in the Acrididae, for example that of *Aiolopus* Fieber by Hollis (1968), the male phallic complex has been found to display considerable uniformity. For this





**Figs 30–35** *Oedaleus* species (females), heads and pronota, dorsal view. 30, *O. nadiae*; 31, *O. roscens*; 32, *O. miniatus*; 33, *O. instillatus*; 34, *O. flavus*; 35, *O. obtusangulus*.



**Figs 36–38** *Oedaleus* species (females), heads and pronota, dorsal view. 36, *O. infernalis*; 37, *O. abruptus*; 38, *O. formosanus*.

reason, although they are described and figures elsewhere in this study, genital characters have not been used to construct a separate key for males. Instead one key is given for both sexes with the main characters derived from the shape and markings of the pronotum, the form of the hind wing fascia, and the colour of the basal area of the hind wing and the interior surface of the hind femur. In addition, characters from the genitalia of either sex are used as subordinate evidence of identification where appropriate.

In these keys total length and head width have been used as subsidiary characters even if the known size-ranges of two taxa partially overlap.

#### African species

- |         |   |  |
|---------|---|--|
| 1       | Hind wing pink or red basally   | 2  |
| –       | Hind wing bright yellow or pale yellow basally  | 3  |
| 2 (1)   | Hind wing with basal area scarlet in male, salmon pink in female, bounded by distinct brown fascia (Fig. 16); antennae flattened, ensiform; male subgenital plate with medial dorso-posterior process (Figs 132, 133) (Somalia, E. Kenya)   | <i>O. miniatius</i> Uvarov (p. 142)                        |
| –       | Hind wing with basal area clear rose pink in both sexes, lacking fascia; antennae filiform; male subgenital plate normal (N. Somalia)   | <i>O. nadiae</i> sp. n. (p. 145)                           |
| 3 (1)   | Hind wing fascia continuous to tip of wing; tegmen unicolorous brown, without pattern (Fig. 8) (Cape Verde Is.)   | melanic form of <i>O. senegalensis</i> (Krauss) (p. 94)    |
| –       | Hind wing fascia forming a distinct band, never continuous to wing tip; tegmen speckled or banded, never unicolorous brown  | 4  |
| 4 (3)   | Hind wing fascia complete, or narrowly interrupted at first anal vein (Figs 9, 11)  | 5  |
| –       | Hind wing fascia broadly interrupted, indistinct, or absent   | 9  |
| 5 (4)   | Hind wing basally bright yellow; dorsal surface of pronotum with small light brown warts (Fig. 34); hind femur internally mauve to deep violet (except E. African males) (S. and E. Africa)   | <i>O. flavus</i> (Linnaeus) (p. 149)                       |
| –       | Hind wing basally pale yellow to colourless; dorsal surface of pronotum smooth; hind femur never mauve or violet internally   | 6  |
| 6 (5)   | Hind femora ventrally straw-coloured; hind margin of pronotum rounded or parabolic  | 7  |
| –       | Hind femora ventrally red or reddish brown; hind margin of pronotum rectangular to obtusangular   | 8  |
| 7 (6)   | Hind margin of pronotum parabolic (Fig. 18); bridge of epiphallus with acutely curved interior surface (Figs 62, 63) (W. Africa to E. Africa N. of 8°S.)  | <i>O. senegalensis</i> (Krauss) (p. 94)                    |
| –       | Hind margin of pronotum oval (Fig. 21); bridge of epiphallus with obtusely curved interior surface (Fig. 68) (Southern Africa S. of 17°S.)  | <i>O. nigrofasciatus</i> (Degeer) (p. 99)                  |
| 8 (6)   | Small species, total length: 22.0–27.5 mm male, 30.0–37.5 mm female; general coloration mottled brown or grey; head, pronotum, and hind femora occasionally pale green suffused with brown, tegmina never tinged with green; white transverse bars on tegmen reduced, not reaching second cubital vein (E. Africa)              | <i>O. instillatus</i> Burr (p. 136)                        |
| –       | Large species, total length: 29.0–45.5 mm male, 42–53 mm female; general coloration variable, green, straw, or brown, always broken up by bands of darker pigment; dorsal surface of folded tegmina suffused with green in green specimens; white transverse bars on tegmina always reaching to second cubital vein (N. Africa) | <i>O. decorus</i> (Germar) (p. 122)                        |
| 9 (4)   | Hind wing fascia absent or only faintly visible   | 10   |
| –       | Hind wing fascia distinctly visible but widely interrupted around first anal vein   | 12   |
| 10 (9)  | Large robust species, total length: 26.8–37.1 mm male, 33.5–48.5 mm female, head width: 4.3–5.4 mm male, 5.8–7.8 mm female (E. Africa)  | <i>O. inornatus</i> Schulthess (p. 147)                    |
| –       | Small species, total length: 22.0–29.0 mm male, 29.0–40.0 mm female, head width: 3.0–4.0 mm male, 4.0–5.5 mm female   | 11   |
| 11 (10) | Pronotal X-marking variable but never absent, posterior arms of X thick (Fig. 22); ventral surface of hind femora red, tegmina exceeding hind knees by one-quarter of femur length or less; female posterior ventral basivalvular sclerite smooth, pale, unsclerotized, lightly pitted (Fig. 45) (Eastern S. Africa)            | extreme form of <i>O. plenus browni</i> subsp. n. (p. 121) |
| –       | Pronotal X-marking thin, often indistinct, sometimes absent; ventral surface of hind femur  |  |

- brown, never red; tegmina exceeding hind knees by one third of femur length or more; female posterior ventral basivalvular sclerite dark, sclerotized, and with rugose warts (Fig. 42) (Madagascar) . . . . . *O. virgula* (Snellen van Vollenhoven) (p. 107)
- 12 (9) Large species, head width 4.5–5.2 mm male, 5.8–7.6 mm female; general coloration pale, uniform, mottled, usually sandy, occasionally suffused with pale green; pronotal X-marking indistinct, pronotal median carina weak, seldom raised, hind margin of pronotum evenly rounded, never angular (Mauritania to Ethiopia) . . . . . *O. johnstoni* Uvarov (p. 109)
- Smaller species, head width 3.5–4.6 mm male, 4.5–6.5 mm female; general coloration darker, with contrasting lighter markings on pronotum and tegmina; pronotal X-marking distinct, pronotal median carina strongly marked, slightly arcuate, hind margin of pronotum angular . . . . . 13
- 13 (12) Tibiae and ventral surface of hind femora straw-coloured, never red . . . . . 14
- Tibiae and ventral surface of hind femora red or orange-red . . . . . 15
- 14 (13) Pronotal hind margin forming an obtuse angle with concave sides (Fig. 23), pronotal X-marking very fine; hind wing fascia strongly marked (Fig. 15) (Southern Africa) . . . . .
- O. carvalhoi* Bolivar (p. 116)
- Pronotal hind margin forming a flat or convex-sided right angle (Fig. 35), pronotal X-marking thicker; hind wing fascia weakly marked (Fig. 3) (Air Mts, Niger, and Arabia) . . . . .
- O. obtusangulus* Uvarov (p. 138)
- 15 (13) Hind margin of pronotum sharply acute, pronotal X-marking very thin; eyes seen from above small and close set, vertex narrow (Fig. 26); dark pattern of tegmina separated into rounded cells; hind wing fascia widely expanded and rounded anteriorly (Fig. 13) (Transvaal) . . . . .
- O. interruptus* (Kirby) (p. 134)
- Hind margin of pronotum bluntly rectangular or obtusangular, pronotal X-marking variable but thicker; eyes normal, more widely set; vertex broader (Figs 20, 22); dark pattern of tegmina forming bands separated by narrow lighter areas; hind wing fascia narrowing or narrowly expanded anteriorly . . . . . 16
- 16 (15) Hind margin of pronotum forming right angle or obtuse angle with concave sides (Fig. 22); hind wing fascia, when complete, not widening in anterior half (Fig. 6), often incomplete, failing to reach second anal vein, occasionally absent (Southern Africa and Tanzania) . . . . .
- O. plenus* (Walker) (p. 118)
- Hind margin of pronotum forming a flat or convex-sided angle (Fig. 20); hind wing fascia widening anteriorly, reaching to second anal vein (Fig. 10) (Senegal to Ethiopia and South to Tanzania) . . . . . *O. nigeriensis* Uvarov (p. 112)

**Non-African species**

- 1 Hind wing fascia complete, or narrowly interrupted at first anal vein (Figs 9, 11) . . . . . 2
- Hind wing fascia broadly interrupted . . . . . 6
- 2 (1) Hind wing basally pale pink (Fig. 4) (Pakistan, NW. India) . . . . . *O. roscens* Uvarov (p. 141)
- Hind wing basally pale yellow, or pale greenish yellow, in *O. decorus* tinged with pale blue at base of main veins . . . . . 3
- 3 (2) Hind wing fascia continuous posteriorly with dark markings at wing tip (Fig. 7); pronotal X-marking indistinct, forming boundary to medial diamond-shaped dark area and merging laterally with lighter markings on sides of pronotum (Fig. 38); tegmen uniformly dark brown, light transverse bands absent or reduced to anterior edge of wing (Taiwan) . . . . .
- O. formosanus* (Shiraki) (p. 132)
- Hind wing fascia not continuous posteriorly with dark markings at wing tip; pronotal X-marking variable, sometimes obscured, but not merging laterally with lighter markings on sides of pronotum; tegmen with two light transverse bands always present . . . . . 4
- 4 (3) Hind margin of pronotum rounded, subarcuate (Fig. 18); ventral surface of hind femur never suffused with red (Arabia, Iran, Pakistan, W. India) . . . . . *O. senegalensis* (Krauss) (p. 94)
- Hind margin of pronotum bluntly obtusangular; ventral surface of hind femora suffused with red . . . . . 5
- 5 (4) Pronotal X-marking sharply outlined, anterior and posterior arms of equal width (Fig. 28); hind wing fascia always dark and well defined (S. Europe, Middle East, U.S.S.R., China, Mongolia) . . . . . *O. decorus* (Germar) (p. 122)



- Pronotal X-marking often indistinct, sometimes absent, posterior arms thicker than anterior arms (Fig. 36); hind wing fascia variable, light brown, edges ill-defined (Fig. 5) (SE. U.S.S.R., E. China, Japan) . . . . . *O. infernalis* Saussure (p. 128)
- 6 (1) Anterior termination of hind wing fascia flattened, reaching or just surpassing second anal vein; fascia, particularly in male, often pale, posterior two thirds parallel to posterior edge of wing; wing narrow (Fig. 2); fastigium of vertex narrow, with lateral carinulae distinct, sharply converging (Fig. 37) (Pakistan, Nepal, India, Bangladesh, Indo-China, China) . . . . . *O. abruptus* (Thunberg) (p. 104)
- Anterior termination of hind wing fascia rounded, surpassing second anal vein, almost reaching first anal vein; fascia distinct, not parallel to edge of wing, wing tip in male heavily clouded; wing normal (Fig. 1); fastigium of vertex broader, carinulae less marked, less convergent (Fig. 27) (SE. New Guinea, Australia, Tasmania) . . . . . *O. australis* Saussure (p. 101)

## Descriptions of the species

### *Oedaleus senegalensis* (Krauss, 1877)

(Figs 8, 9, 18, 40, 60–65, 160)

*Pachytylus senegalensis* Krauss, 1877: 56. Syntypes ♂♀, SENEGAL: St Louis & Dagana (*F. Steindachner*) (lost). NEOTYPE ♂, SENEGAL (BMNH), here designated [examined].

*Ctypohippus arenivolans* Butler, 1881: 85. Holotype ♀, CAPE VERDE IS. (BMNH) [examined]. [Synonymized by Kirby, 1910: 225.]

*Pachytylus mlokozewitzcki* Bolívar, 1884: 105. LECTOTYPE ♂, U.S.S.R.: Tiflis (MHN, Geneva), here designated [examined]. [Synonymized by Uvarov, 1921: 487.]

*Oedaleus mlokosiewitchi* (sic) (Bolívar) Bolívar, 1887: 98; Jacobson & Bianchi, 1902: 256.

*Oedaleus* (*Oedaleus*) *mlokozievetsi* (sic) (Bolívar); Saussure, 1888: 40.

*Oedaleus* (*Oedaleus*) *mlokozievetzi* (sic) (Bolívar); Saussure, 1888: 42.

*Oedaleus* (*Oedaleus*) *senegalensis* var. *c.* Saussure, 1888: 42; Uvarov, 1921: 487.

*Oedaleus mlokosiewiczi* (sic) (Bolívar); Jacobson & Bianchi, 1902: 188.

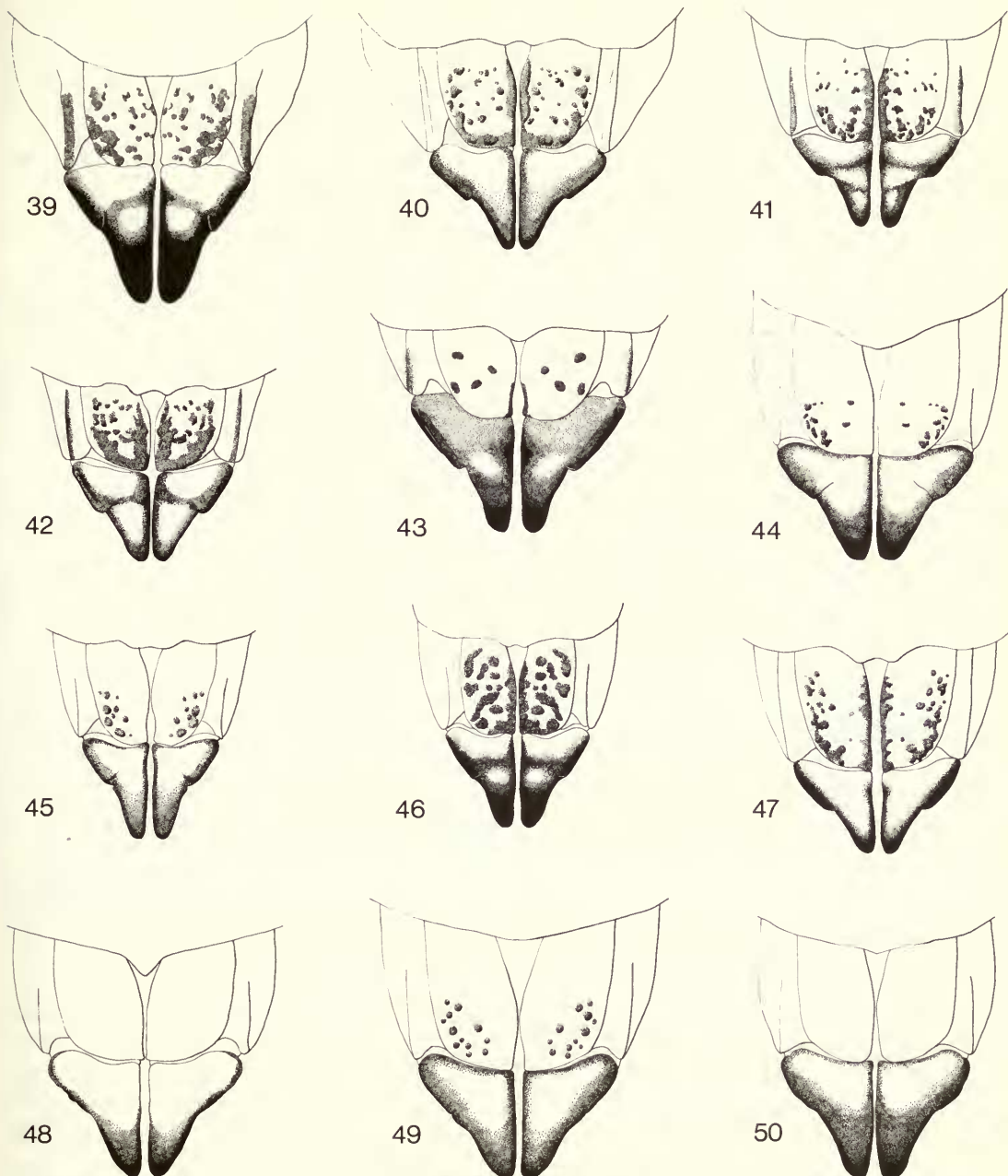
*Oedaleus senegalensis* (Krauss); Bolívar, 1889: 104.

*Oedaleus senegalensis* var. *dimidiatus* Bolívar, 1889: 105. Holotype ♀, CAPE VERDE IS. (MLZA, Lisbon) [examined]. **Syn. n.**

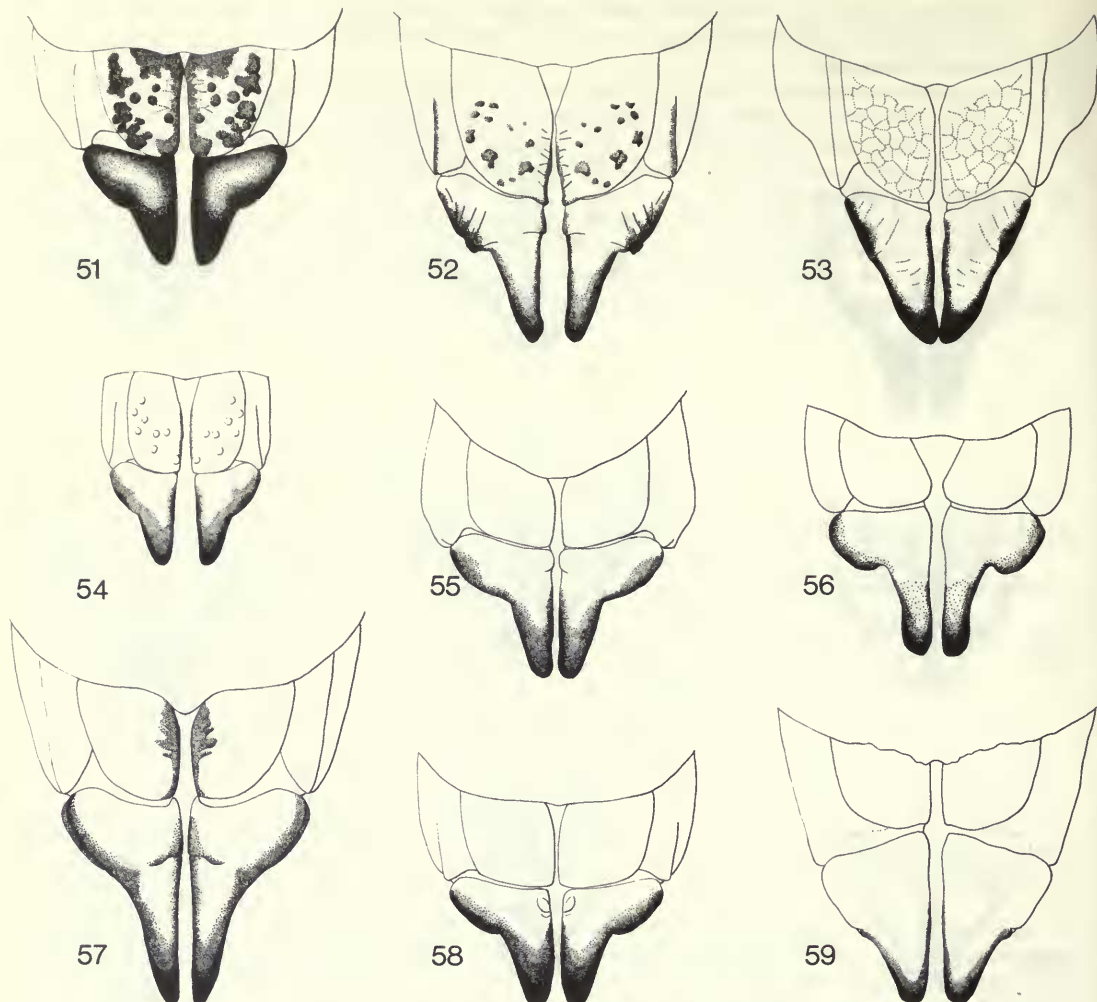
REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae up to twice as long as head and pronotum together, flagellum with 24–26 segments. Fastigium little longer than wide, concave, narrowing to little less than half of maximum width anteriorly, margins raised; frons in profile, slightly convex; frontal ridge barely constricted ventral to median ocellus. Eyes little less than one and a half times as deep as wide. Pronotum low tectiform; median carina arcuate, not or barely intersected by posterior sulcus; hind margin subarcuate. Tegmen surpassing folded hind knees by one-third to one-half length of hind femur. Hind tibia with 13 inner and 12–13 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice claw length; arolium half claw length. Cerci one and three quarter times as long as basal width. Genitalia (Figs 60–64): cingular apodemes moderate length and thickness; rami fully developed, with exposed portion of cingular and apical penis valves short, subapical ventral process rounded; epiphallus rectangular with narrow bridge; inner lobes of lophi more than twice as wide as outer; anterior projections large, rounded; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum, and dorsal surface of folded tegmina and hind femora. Tegmen infusate brown in basal two-fifths, with strong transverse pale band reaching first anal vein one-third along from base; indistinct pale transverse band sometimes visible one-sixth along from base; apical two-fifths of tegmen clear with occasional infumate cells bordered by darkened veins. Hind wing fascia (Fig. 9) complete, sometimes narrowly interrupted between second cubitus and first anal vein, not reaching hind margin of wing; basal area pale yellow, apex very slightly speckled with infumate cells. Hind femora with three indistinct oblique transverse dark bands on outer upper marginal and medial areas extending onto inner surface; ventral surface pale straw-coloured; hind knee dark brown; hind tibia with dark basal ring, subbasal pale straw area then straw shaded with brown and distally pinkish.

♀. Ventral ovipositor valves (Fig. 40) short, well sclerotized. Spermatheca (Fig. 65) with apical diverticulum elongate with short, blunt subapical diverticulum.



**Figs 39–50** *Oedaleus* species, ventral ovipositor valves, ventral view. 39, *O. nigeriensis*; 40, *O. senegalensis*; 41, *O. nigrofasciatus*; 42, *O. virgula*; 43, *O. johnstoni*; 44, *O. carvalhoi*; 45, *O. plenus*; 46, *O. interruptus*; 47, *O. australis*; 48, *O. abruptus*; 49, *O. flavus flavus*; 50, *O. flavus somaliensis*.



Figs 51–59 *Oedaleus* species, ventral ovipositor valves, ventral view. 51, *O. decorus*; 52, *O. infernalis*; 53, *O. formosanus*; 54, *O. roscens*; 55, *O. obtusangulus*; 56, *O. instillatus*; 57, *O. inornatus*; 58, *O. nadiæ*; 59, *O. miniatus*.

#### MEASUREMENTS

Sample from Niger: Danga, at light, 7.viii.74 (J. M. Ritchie).

#### Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27.35	3.87	3.64	20.79	12.57	2.73	4.61	5.71
Range	23.5–30.4	3.4–4.5	3.1–3.4	17.3–23.4	11.1–14.4	2.3–3.1	4.3–5.0	5.0–6.2
S.D.	2.127	0.236	0.278	1.783	0.932	0.175	0.197	0.266
n	24	29	29	24	28	28	28	24



## Females

Mean	35.38	5.04	4.55	26.97	15.61	3.3	4.74	5.96
Range	30.3– 39.0	4.4– 5.5	3.6– 5.3	23.2– 30.0	13.3– 17.7	2.9– 3.8	4.1– 5.1	5.3– 6.6
S.D.	1.726	0.222	0.33	1.493	0.807	0.201	0.216	0.317
n	42	45	45	42	45	45	45	42

Sample from Niger: Danga, at light, 12.ix.74 (*J. M. Ritchie*).

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	32.64	4.60	4.56	24.56	15.53	3.39	4.59	5.44
Range	31.2– 34.8	4.2– 5.0	4.1– 5.1	22.7– 26.7	13.2– 17.1	3.0– 3.7	4.2– 4.8	4.8– 5.9
S.D.	1.15	0.231	0.295	1.042	0.879	0.156	0.139	0.499
n	18	19	19	18	20	20	20	18

## Females

Mean	42.39	6.12	5.77	32.16	19.6	4.28	4.58	5.99
Range	40.4– 46.9	5.7– 6.5	5.1– 6.5	30.7– 35.2	17.7– 21.3	3.9– 4.6	4.2– 5.0	4.9– 6.0
S.D.	1.551	0.204	0.382	1.095	0.938	0.199	0.189	0.295
n	20	20	20	20	20	20	20	20

**AFFINITIES.** *O. senegalensis* is most closely allied to *O. nigrofasciatus* from southern Africa. They may be distinguished with difficulty on grounds of size, pronotal shape (Figs 18, 21), and the shorter anal cerci of male *senegalensis* (Fig. 64). Both species belong to a close-knit group of species characterized by an epiphallus having lophi with large, transverse, inner lobes much larger than the outer lobes.

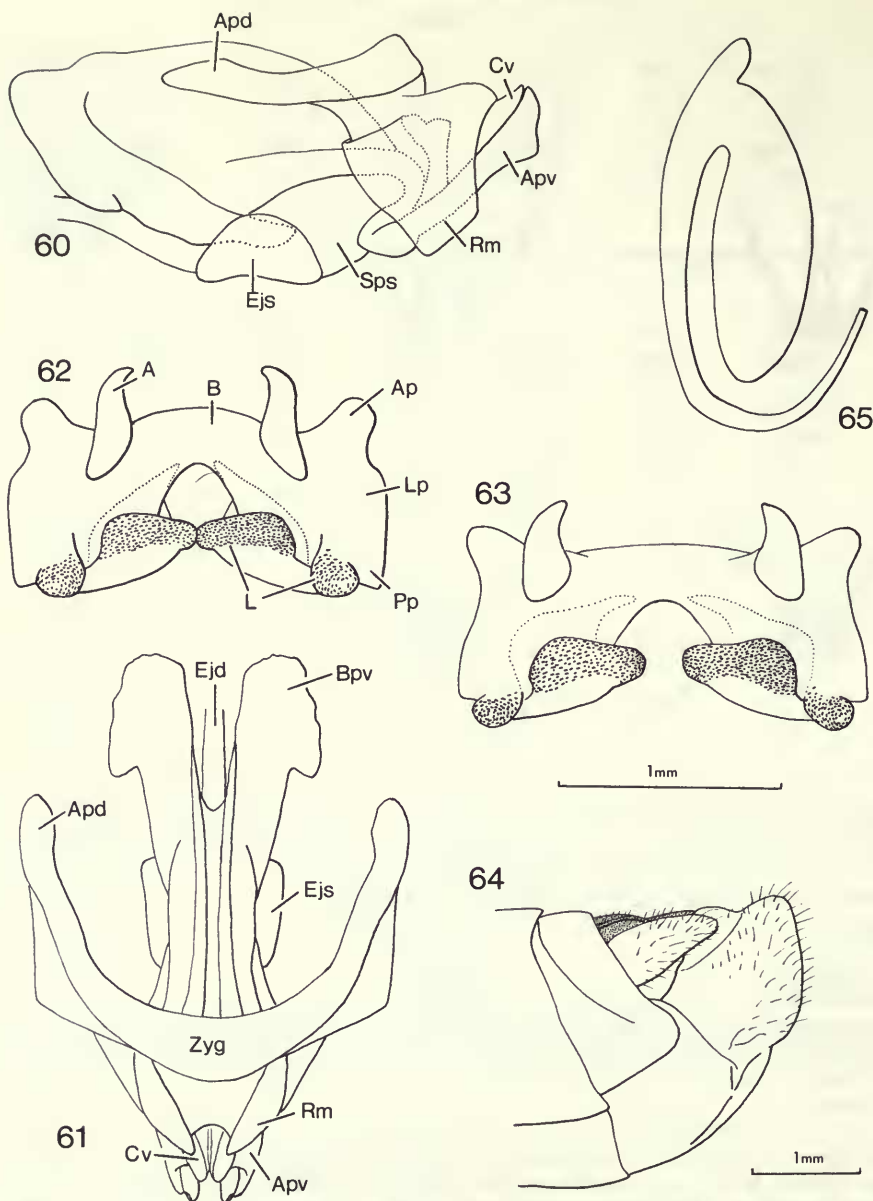
## MATERIAL EXAMINED

*Pachytylus senegalensis* Krauss, neotype ♂, **Senegal**: Dakar airport, at light, 6.x.1974 (*Ritchie*) (BMNH). *Ctyophippus arenivolans* Butler, holotype ♀, **Cape Verde Is.**: St Vincent I., from sandy patches, 24.x.1878 (*Butler*) (BMNH). *Pachytylus mlokoziewitzcki* Bolivar, lectotype ♂, **U.S.S.R.**: Tibilisi ('Tiflis'), no further data (MHN, Geneva). *Oedaleus senegalensis* var. *dimidiatus* Bolivar, holotype ♀, **Cape Verde Is.**: (*Ferreira Borges*) (MLZA, Lisbon).

In addition to the primary type-material listed above, more than 3500 specimens were examined from the following countries: **Canary Is.**, **Cape Verde Is.** (including material of var. *dimidiatus*), **Gambia**, **Senegal**, **Mauritania**, **Algeria**, **Mali**, **Niger**, **Nigeria**, **Sudan**, **Ethiopia**, **Somali Republic**, **Kenya**, **Tanzania**, **Socotra**, **Yemen**, **Saudi Arabia**, **Kuwait**, **Qatar**, **Israel**, **Jordan**, **Syria**, **Iran**, **Afghanistan**, **Pakistan**, **India**.

**DISTRIBUTION** (Fig. 160, and Biogeography section, p. 162). From the Canary Is. in the west, across north and subsaharan Africa, into the western U.S.S.R. in the north-east and western India in the south-east.

**BIOLOGY.** The available data on the life history, distribution, ecology, and economic importance of this species were reviewed by Batten (1969). More recently Lecoq (1978) has investigated the life cycle in relation to migration in Upper Volta, and Launois (1979) has advanced a theoretical model of the annual cycle consisting of three generations with latitudinal movements governed by the Intertropical Convergence Zone. Launois-Luong (1976) has made estimates of fecundity by a detailed study of the ovaries and Cheke, Fishpool & Ritchie (1980) have studied the distribution and predation of egg pods, giving descriptions of the pod, the eggs, and oviposition behaviour. The influence of rainfall in terminating egg diapause has been investigated by Venkatesh et al. (1971). The



**Figs 60–65** *O. senegalensis*, genitalia. 60, endophallus and cingulum, lateral view; 61, same, dorsal view; 62, 63, variation in epiphallus shape; 64; apex of male abdomen, lateral view; 65, spermatheca.

occurrence of large numbers of *O. senegalensis* out at sea off the West African coast has been documented by Ritchie (1978a). The thoracic repugnatorial gland has been described by Vosseler (1902c), and the causes of colour change by Abushama & El Khider (1973). Several birds are known to prey on this species including the carmine bee-eater, *Merops nubicus* (Nickerson, 1958), the Abyssinian roller, *Coracias abyssinicus* (Roy, 1970), and the cattle egret, *Ardeola ibis* (pers. obs.). Since 1973 there have been several unpublished reports describing crop damage and aspects of the biology of *O. senegalensis* (Popov, 1974; McAleer, 1977; Page, 1977).

DISCUSSION. The variety *dimidiatus* Bolívar from the Cape Verde Is. is here synonymized on the grounds that it is sympatric with the normal form of *O. senegalensis* and almost certainly constitutes a melanic variant rather than a good subspecies. A fuller treatment of this subject with measurements of the two forms have been given elsewhere (Ritchie, 1978a). The measurements given above for this species form part of a study of the morphometric changes in this species during the 1974 rainy season in north-western Niger (Ritchie, unpubl.). They illustrate the considerable size differences which may be encountered in this species within a small geographical area over a short period of time.

The type-material of *Pachytylus mlokoziewitzki* Bolívar comprises one male, here designated lectotype, and one female, designated paralectotype.

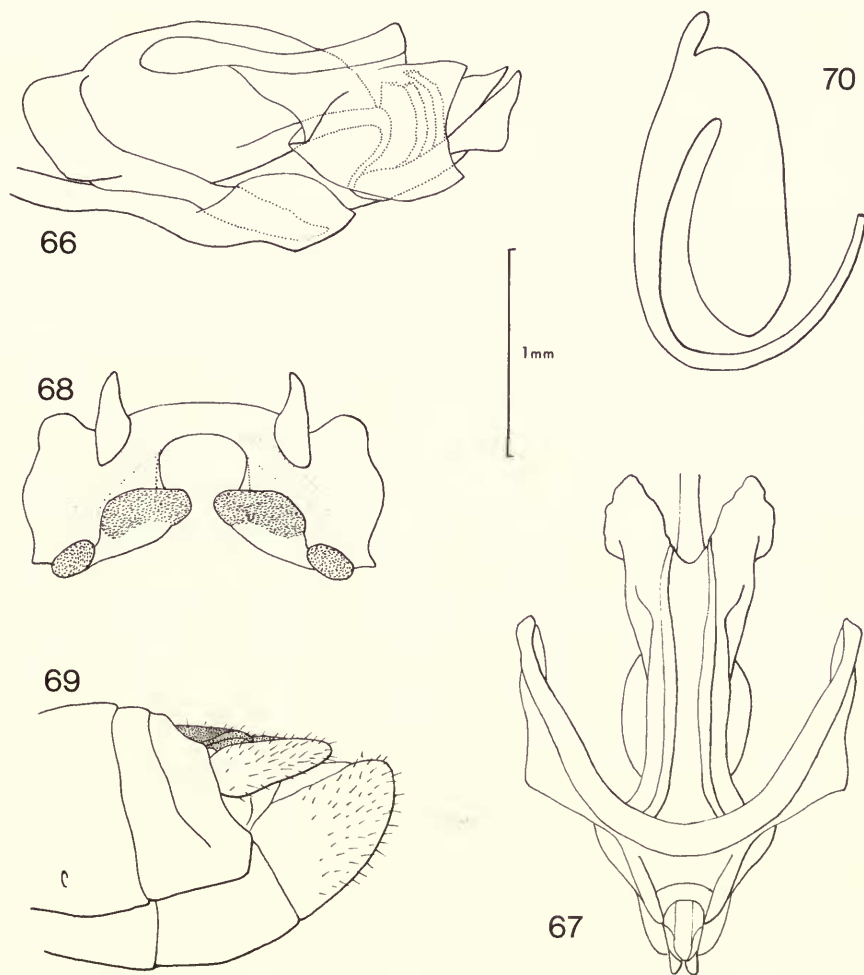
***Oedaleus nigrofasciatus* (Degeer, 1773)**

(Figs 21, 41, 66–70, 152)

*Acrydium nigrofasciatum* Degeer, 1773: 493. Holotype ♀, SOUTH AFRICA (NR, Stockholm) [examined].

*Gryllus arcuatus* Thunberg, 1824: 409. LECTOTYPE ♂, no data (ZIUU, Uppsala) here designated [examined] [Synonymised by Stål, 1873: 126.]

*Pachytylus nigrofasciatus* (Degeer) Schaum, 1853: 776. [Partly confused with *Oedaleus decorus* (Germar).]



**Figs 66–70** *O. nigrofasciatus*, genitalia. 66, endophallus and cingulum, lateral view; 67, same, dorsal view; 68, epiphallus; 69, apex of male abdomen, lateral view; 70, spermatheca.



- Pachytylus (Oedaleus) nigro-fasciatus* (Degeer); Stål, 1873: 126. [Partly confused with *Oedaleus decorus* (Germar).]  
*Oedaleus (Oedaleus) nigro-fasciatus* (Degeer) Saussure, 1884: 116.  
*Oedaleus (Oedaleus) nigro-fasciatus* var. *gracilis* Saussure, 1884: 116. LECTOTYPE ♀, SOUTH AFRICA: Cape of Good Hope (MHN, Geneva), here designated [examined]. [Partly confused with *Oedaleus decorus* (Germar).] [Synonymized by Uvarov, 1923: 69.]  
*Oedalus* [sic] *nigrofasciatus* (Degeer); Distant, 1892: 260.  
*Oedaleus nigrofasciatus* var. *gracilis* Saussure; Saussure, 1893: 581.  
*Oedaleus nigrofasciatus* (Degeer); Brancsik, 1900: 182.  
*Oedaleus nigrofasciatus* (Degeer); Kirby, 1910: 224. [Partly confused with *Oedaleus decorus* (Germar).]  
*Oedaleus gracilis* Saussure; Uvarov, 1922: 102.

REDESCRIPTION. ♂. Integument finely rugulose and punctate. Antennae one and a half times as long as head and pronotum together; flagellum with 23 segments. Fastigium longer than wide, concave with lateral margins distinct and convergent posteriorly, narrowing to two-fifths of maximum width anteriorly; frons in profile slightly convex; frontal ridge slightly expanded at median ocellus, becoming obsolete ventrally. Eyes about one and a half times as deep as wide. Pronotum low tectiform; median carina arcuate, often finely intersected by posterior sulcus; hind margin rounded obtusangular. Tegmen surpassing folded hind knees by one-third to one-half of hind femur length. Hind tibiae with 12 inner and 11 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a quarter times claw length; arolium three-fifths of claw length. Cerci twice as long as basal width. Genitalia (Figs 66–69): cingular apodemes thin, moderately long and curved; rami elongate dorsally; exposed portion of cingular and apical penis valves short; subapical ventral process angular; epiphallus rectangular with narrow bridge, inner lobes of lophi twice as wide as outer lobes; anterior projections large and rounded, posterior projections small and acute.

General coloration variable, brown, with lighter brown, ochraceous, or green markings on frons, vertex, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infusate brown in basal half with three irregular pale transverse bands at intervals of one-sixth, one-third, and one-half, along from base, basal band often obsolete; apical half clear with small variable brown patches. Hind wing fascia as in *O. senegalensis*, continuous, not touching hind margin; wing tip with irregular pattern of brown cells; basal area pale yellow. Hind femur with three dark brown variable oblique transverse bands on external medial, upper marginal, and interior upper marginal areas, obsolescent on interior medial area; ventral surface mid brown, hind knees dark brown to black; hind tibiae with dark basal ring, subbasal pale area, otherwise fawn.

♀. Ventral ovipositor valves (Fig. 41) short, moderately sclerotized, slightly incurved on external lateral surface. Spermatheca (Fig. 70) with finger-like subapical diverticulum.

#### MEASUREMENTS

Sample from South Africa: Cape Province, various localities.

#### Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26.52	3.47	3.89	20.17	12.44	2.85	4.38	5.20
Range	23.3–30.2	3.1–3.9	3.1–4.8	17.5–23.5	10.8–13.8	2.4–3.2	4.05–4.6	4.6–5.9
S.D.	1.557	0.190	0.383	1.295	0.766	0.182	0.164	0.299
n	27	26	27	27	27	27	27	27

#### Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	32.99	4.58	4.97	25.15	15.67	3.48	4.50	5.07
Range	29.8–35.6	4.2–4.9	4.3–5.6	22.7–27.0	13.8–17.2	3.0–3.8	4.2–4.8	4.7–5.7
S.D.	1.755	0.208	0.375	1.375	0.964	0.202	0.189	0.255
n	13	13	13	13	13	13	13	13

AFFINITIES. *O. nigrofasciatus* is most closely allied to *O. senegalensis* under which species heading the principal similarities are described (p. 97).

## MATERIAL EXAMINED

*Acrydium nigrofasciatum* Degeer, holotype ♀, **South Africa**: Cape of Good Hope, no further data (NR, Stockholm). *Gryllus arcuatus* Thunberg, lectotype ♂, no data (ZIUU, Uppsala). *Oedaleus nigrofasciatus* var. *gracilis* Saussure, lectotype ♀, **South Africa**: Cape of Good Hope, no further data (MHN, Geneva).

In addition to the primary type-material listed above, 211 specimens were examined from the following localities. **South Africa**: Transvaal, Reitspruit; T., Johannesburg; T., Pretoria; T., Zeerust, Morico; 32.2 km NE. of Pretoria; T., 96.6 km NE. of Ermelo; T., Lydenburg distr.; T., Waterburg distr.; T., Platrivier; T., Potchefstroom; T., Makokoane; Orange Free State: Bloemfontein to Port Elizabeth; O.F.S., Bloemfontein; O.F.S., Boshof; O.F.S., Witzieshoek, 1830 m; North Bank Halt, Norvals Pont; O.F.S., Ficksburg; Natal, Zululand, Nqutu; N., Natal National Park; Cape Province, Middleburg; C.P., Knysna, Plettenburg Bay; C.P., Albert distr., Simonstown; C.P., Ceres; C.P., Worcester; C.P., Aliwal North; C.P., Rondenbosch; C.P., Contour Path; C.P., Huguenot; C.P., Traddow Pass; C.P., Mafeking; C.P., Swellendam; C.P., Cape Peninsula, Signal Hill; C.P., Newlands; C.P., Mossel Bay; C.P., Kirstenbosch; C.P., Du Toit's Kloof, nr Paarl; C.P., Waterval-Onder; C.P., Namaqualand; C.P., 20 km SW. of Mitchell's Pass; C.P., Highlands, Grabon; C.P., Stellenbosch; C.P., Hopetown; C.P., Citrusdale to Clan William road. **Namibia**: Okahandja; Okahandja to Waterberg; 17°59'S, 16°02'E, 1110m; Rietfontein, 19°50'S, 17°52'E; Otjikoko Süd Farm, 53.1 km ENE. of Omaruru; Otjitambi Farm, 43.5 km ESE. of Kamanjab; Hoffnung Farm, 16.1 km NE. of Windhoek. **Botswana**: Lobatsi; Ghanzi; Mongalatsiba; Kwebe Hills; Ngamiland; Gaborones; Kuke Pan; Kaotwe; Metsimaklaba. **Zimbabwe**: Odzi distr.; Selukwe, 1420 m; Matopo Hills; Mutambara; West Nicholson, Masase.

**DISTRIBUTION** (Fig. 152, and Biogeography section, p. 156). Widely distributed and common throughout southern Africa south of the *Brachystegia* woodland.

**BIOLOGY.** *O. nigrofasciatus* has been studied in the Karroo where Reyneke (1941) noted that the species has similar habitat preferences to the brown locust *Locustana pardalina* (Walker). It was found in open sandy or pebbly patches with short grass and scattered shrubs at an average density of five insects per square metre. Nymphs were seen from the end of September until November. In the Cape peninsula Key (1930) found adults from November to June and observed oviposition from January to June. Egg pods were 21–24 mm long with 15–19 eggs, and were usually curved and medially constricted. In Johannesburg Chesler (1938) found somewhat larger pods, about 29 × 5 mm with 20–25 eggs in rows of four. Chesler described the five nymphal instars which occupied an average of 80 days for their completion. She postulated a two-generation cycle with eggs hatching in September to produce adults November–December whose eggs hatched in January to give a second generation of adults in April. These adults then lay eggs which remain in the soil until the next rains in September. Nolte (1939) compared the biology of *O. nigrofasciatus* with six other common species of grasshopper including *O. carvalhoi*. He reported that adult females of *O. nigrofasciatus* have 15 ovarioles per ovary. Both *Oedaleus* species were found to have the standard acridid complement of 11 pairs of autosomes and an XO sex determination system. There is one record of damage to tobacco seedlings in Rhodesia (Bünzli & Buttiker, 1956).

**DISCUSSION.** The type-series of *Gryllus arcuatus* Thunberg comprises one male, here designated lectotype, and one female, designated paralectotype. *O. nigrofasciatus* var. *gracilis* Saussure was described from South Africa and south Russia. In the MHN, Geneva, there are two males and two females labelled as *gracilis* from South Africa as well as several specimens from Russia which are actually *O. decorus*. A single female from South Africa bears the labels 'Cap. B. Esp.' and '*nigrofasciatus* Th. var. *gracilis* Sss. Afr.', apparently in Saussure's own handwriting. This specimen is here designated lectotype. No paralectotypes have been designated because of uncertainty as to whether Saussure himself named the remaining specimens when he was describing var. *gracilis*.

*Oedaleus australis* Saussure, 1888

(Figs 1, 27, 47, 71–74, 164)

*Oedaleus (Oedaleus) senegalensis* var. *d.* Saussure, 1884: 117; Uvarov, 1930*d*: 599.*Oedaleus (Oedaleus) nigro-fasciatus* var. *australis* Saussure, 1888: 41. LECTOTYPE ♀, AUSTRALIA (MHN, Geneva), here designated [examined].[*Oedaleus senegalensis* var., Froggatt, 1903: 1105. Misidentification; Uvarov, 1930*d*: 599.][*Oedaleus senegalensis* Krauss; Froggatt, 1907: 539; 1910: 7. Misidentifications: Uvarov, 1930*b*: 599.]

*Oedaleus australis* Saussure; Kirby, 1910: 225.

[*Oedaleus senegalensis* Krauss; Sjöstedt, 1920: 11. Misidentification; Uvarov, 1930*d*: 599.]

[*Oedaleus senegalensis* Krauss; Sjöstedt, 1921: 53. Misidentification.]

[*Oedaleus senegalensis* Krauss; Zacher, 1925: 204; 1949: 298. Misidentifications; Batten, 1969: 29.]

*Oedaleus australis* var. *plana* Sjöstedt, 1931*a*: 2. Holotype ♀, AUSTRALIA: A.C.T., Canberra, 20.ii.29 (Fuller) (ANIC, Canberra). **Syn. n.**

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae about one and a third times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to less than one third of maximum width anteriorly, with well-defined lateral carinae; frons in profile slightly convex; frontal ridge slightly expanded at median ocellus. Eyes about one and a third times as deep as wide. Pronotum low tectiform; median carina arcuate, narrowly intersected by posterior sulcus; hind margin of pronotum rounded obtusangular. Tegmen surpassing folded hind knees by one-quarter to one-half of hind femur length. Hind tibia with 11 inner and outer spines; inner apical spurs twice as long as outer; apical tarsal segment three times length of claw; arolium one-third length of claw. Cerci little more than twice as long as basal width. Genitalia (Figs 71–73) with cingular apodemes long, thin, strongly curved; rami fully developed, with exposed portion of cingular and apical penis valves short; subapical ventral process small; epiphallus rectangular with narrow bridge; inner lobes of lophi nearly twice as wide as outer; anterior projections large, rounded acutangular; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infusate brown in basal half with irregular pale transverse band extending from costal margin to second anal vein posteriorly, situated one-third along from base; indistinct secondary band sometimes visible one-sixth along from base; apical half of tegmen clear with variable brown patches. Hind wing fascia (Fig. 1) narrowly interrupted at first anal vein, not reaching hind margin of wing; wing tip infusate brown, basal area of wing pale yellow. Hind femora with three indistinct dark, variable, oblique transverse bands on outer and inner upper marginal and medial areas; ventral surface of hind femur straw-coloured; hind knees blackish; hind tibiae with dark basal ring, subbasal pale area, otherwise light brown.

♀. Frons in profile convex. Ventral ovipositor valves (Fig. 47) short, strongly sclerotized, with strongly curved apices. Spermatheca (Fig. 74) with apical diverticulum acutely rounded distally and finger-like subapical diverticulum.

#### MEASUREMENTS (all available material)

##### Males

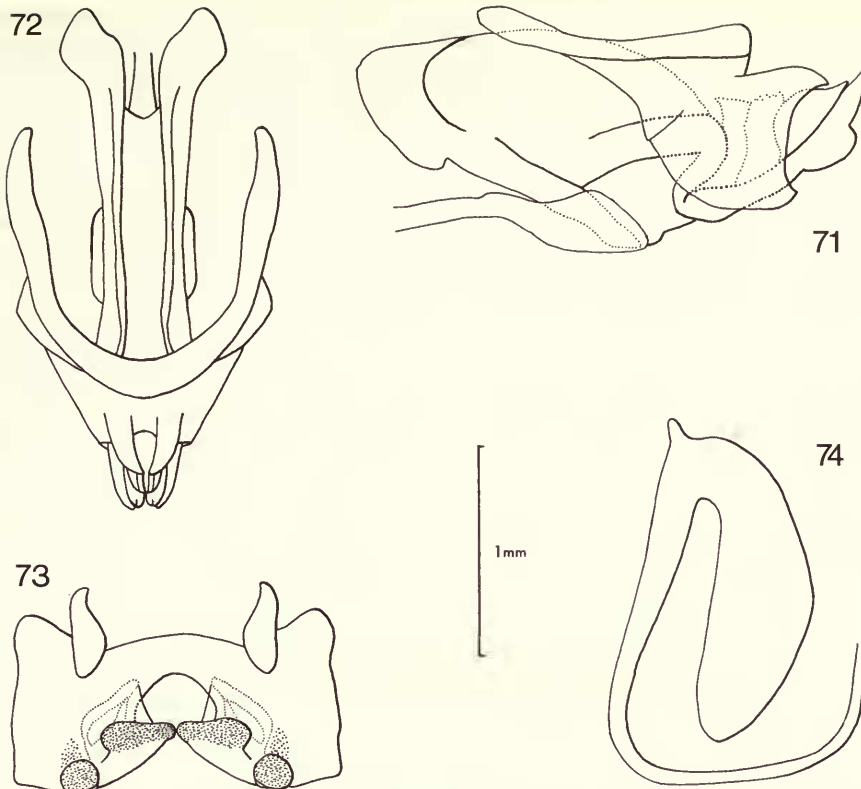
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	24.13	3.71	3.73	17.59	12.5	3.05	4.11	4.74
Range	20.0–27.8	3.1–4.1	2.8–4.2	14.2–20.9	10.5–14.3	2.6–3.5	3.7–5.0	3.8–5.6
S.D.	2.371	0.299	0.377	2.034	1.085	0.223	0.347	0.539
n	11	12	12	12	12	12	12	12

##### Females

Mean	31.09	4.93	4.99	23.02	15.3	3.8	4.03	4.63
Range	28.6–34.5	4.2–5.6	3.7–6.1	20.0–26.2	13.6–16.6	3.3–4.2	3.8–4.2	4.2–5.3
S.D.	1.712	0.305	0.479	1.562	0.84	0.222	0.113	0.328
n	18	22	21	21	21	21	21	21

AFFINITIES. *O. australis* is most closely allied to *O. senegalensis* and *O. nigrofasciatus* which it very closely resembles in most respects, and with which it was originally confused. It may be distinguished by its smaller size, the interrupted band of the hind wing (Fig. 1), and the relatively short tegmen and correspondingly low TL/PL ratio.





Figs 71–74 *O. australis*, genitalia. 71, endophallus and cingulum, lateral view; 72, same, dorsal view; 73, epiphallus; 74, spermatheca.

#### MATERIAL EXAMINED

*Oedaleus nigrofasciatus* var. *australis* Saussure, lectotype ♀, **Australia** (MHN, Geneva). *Oedaleus australis* var. *plana* Sjöstedt, holotype ♀, **Australia**: A.C.T., Canberra, 20.ii.1929 (Fuller) (ANIC, Canberra).

**Australia**: 1 ♂, Queensland, 20.9 km E, 3 mls N. of Candamine, Nangram lagoon, 14.viii.1954 (Stirton) (CAS, San Francisco); 1 ♂, N. Queensland, Ravenshoe–Mt Garnet road, Archer's Creek, 11.i.1962 (Britton); 2 ♀, Queensland Dept. Agric., 1954; 2 ♀, Queensland (Waterhouse); 1 ♀, N. Queensland, Inkerman, nr Townsville; 1 ♀, Queensland, Peak Downs (MNHU, Berlin); 1 ♀, Queensland, Proserpine, 7.ii.1964 (Sedlacek) (BPBM, Hawaii); 1 ♀, Queensland, 24 km S. of Sarina, 7.ii.1964 (Sedlacek) (BPBM, Hawaii); 1 ♀, Queensland, Kuranda, 1904 (Perkins & Koebele) (BPBM, Hawaii); 1 ♂, Queensland, Brisbane, 16.ii.1915 (Hacker) (MNHU, Berlin); 1 ♂, Queensland, 24.2 km from Brisbane, Acacia Ridge, 6.iv.1966 (Grant); 1 ♂, N.S.W., Shoalhaven R., 27.xi.1948 (Britton); 4 ♂, 2 ♀, 1 nymph, 4.8 km W. of Cooma, 28.i.1962 (Britton); 1 ♀, N.S.W., Cadramatta, at light, 10.iii.1959 (Nikitin); 1 ♀, N.S.W., Cadramatta, 11.xii.1957 (Nikitin); 1 ♀, same data, 1.iii.1958; 2 ♀, N.S.W., Sydney, 26.ii.1902; 1 ♂, 1 ♀, N.S.W., Woy Woy, 8.iii.1924 (Nicholson); 1 ♀, N.S.W., Clarence R., (Lea); 1 ♂, N.S.W., S. of Coonamble, flat plain pasture, 22.xi.1969 (Lambert); N.S.W., Trangie, at light, 1.xii.1969 (Lambert); 2 ♀, 4.83 km NE. of Trangie, *E. populifolia* wood and pastureland, 28.xi.1969 (Lambert); 1 ♀, W. central N.S.W., Hillside, NE. of Trangie, at light, 25.xi.1969 (Cameron); 1 ♀, N.S.W., no further data (MHN, Geneva) (paralectotype of *O. nigrofasciatus* var. *australis* Saussure); 2 ♀, A.C.T., Paddy's Creek, 25.xii.1965 (Richards); 1 ♀, Paramatta, no further data. **Tasmania**: 1 ♂, no further data (Lea). **New Guinea**: 1 ♂, Variatara distr., Port Moresby, 18.iii.1956 (Brown).

**DISTRIBUTION** (Fig. 164, and Biogeography section, p. 165). Common throughout the eastern half of Australia, and Tasmania. The species is newly recorded here from New Guinea. Additional data for the distribution map have kindly been provided by Dr K. H. L. Key, from specimens in the Australian National Insect Collection, Canberra.

BIOLOGY. Little is known of the biology of *O. australis*. There are probably at least two generations with eggs surviving the dry season April–September, since adults and nymphs have mainly been recorded September–March. However, adults do occur in all months in suitable localities (ANIC specimens). Large swarms were recorded damaging pasture at Singleton, N.S.W., in 1906–7 (Froggatt, 1907). There was a heavy incidence of an unspecified dipterous parasite. Eggs were laid in well-defined egg beds. In a later account (Froggatt, 1910) egg pods were said to be laid about 32 mm deep in hard clay soil on open grassy ridges with 30–50 eggs per pod. *O. australis* has been recorded among the stomach contents of the straw-necked ibis, *Threskiornis spinicollis* and the white ibis, *T. molucca* (Carrick, 1959). It seems that this species rarely achieves swarm densities.

DISCUSSION. The type of *O. australis* var. *plana* was generally supposed to be at Stockholm. However, I am indebted to Dr Key for the following information:

‘There is indeed in Stockholm a specimen determined as *plana* by Sjöstedt and bearing his “Typus” label. But it came from Colosseum, Qld., whereas the only locality given for *plana* in the brief original description of 1931 (under “*Oedaleus senegalensis*”) mentions only one locality, namely “Canberra”. Thus the Stockholm “type” is not even a syntype. However, the ANIC does have a single female bearing the capture data essentially as cited by Sjöstedt, namely “Canberra F.C.T. 20 Feb. 1929 M. Fuller”. It bears also the following labels: (1) “*Oedaleus australis* var. *recta* [sic] Sjöstedt det.”, and (2) “*Oedaleus senegalensis* Kr. ♀ Yngve Sjöstedt det.” The name “*recta*” is a *nomen nudum* and clearly a lapsus for “*plana*”, described as “mit *geradem* Kiel des Pronotums.” In the absence of evidence that Sjöstedt had more than one specimen before him, the Canberra female, being the only one to bear the required capture data, must be accepted as the holotype. I have now added the following label: “HOLOTYPE ANIC 8747. *Oedaleus australis* var. *plana* Sjöstedt, 1931. ♀”, on red fluorescent card.’

Saussure (1884; 1888) was clearly never able satisfactorily to separate *O. senegalensis*, *O. nigrofasciatus*, and *O. nigrofasciatus* var. *australis*. In his 1884 work he mentioned material of *O. senegalensis* from ‘Australia’ which must be *australis* and in 1888 he described *O. nigrofasciatus* var. *australis* from ‘Nov. Holland’ but also listed a var. *a* of *O. senegalensis* from ‘Australia’ and a var. *c* from ‘Nov. Holl.’, both of which are clearly conspecific with *australis*. Neither of the two female specimens of *australis* in Saussure’s collection at Geneva is labelled as such. Instead one is labelled ‘*O. senegalensis* Kr.’ and the other ‘*Acridium maculatum* Br.’ Both are labelled as from Australia, not ‘Nov. Holland’. It is possible that Saussure never labelled any material as var. *australis* since his curatorial practice was very variable and he may in any case have been unsure of the identity of his material. Accordingly the female misidentified as *O. senegalensis* is here designated lectotype of *O. nigrofasciatus* var. *australis* and the other female is designated paralectotype.

### *Oedaleus abruptus* (Thunberg, 1815)

(Figs 2, 37, 48, 75–78, 157)

*Gryllus abruptus* Thunberg, 1815: 233. LECTOTYPE ♂, CHINA (ZI, Uppsala) here designated [examined].

*Pachytylus (Oedaleus) abruptus* (Thunberg) Stål, 1873: 127.

*Oedaleus (Oedaleus) abruptus* (Thunberg) Saussure, 1884: 117.

*Oedaleus abruptus* (Thunberg); Kirby, 1910: 226.

[*Oedaleus nigrofasciatus* (Degeer); Barber & Jones, 1915: 163; Gabriel, 1968: 101. Misidentifications.]

REDESCRIPTION. ♂. Unusually small species. Integument finely rugulose and pitted. Antennae about one and one-third times as long as head and pronotum together; flagellum with 20 segments. Fastigium of vertex longer than wide, concave, narrowing to two-fifths of maximum width anteriorly, with distinct lateral carinae; frons in profile slightly convex; frontal ridge constricted just below median ocellus, becoming obsolescent ventrally. Eyes about one and two-fifths as long as wide. Pronotum low tectiform; median carina low arcuate, not intersected by posterior sulcus; hind margin rounded obtusangular. Tegmen surpassing folded hind knees by about one-third of hind femur length with numerous long fine hairs on subcostal and radial veins. Hind tibia with 13 inner and 12 outer spines; inner apical spurs one and four-fifths as long as outer, apical tarsal segment twice claw length; arolium three-fifths length of claw; outer surface of ventral inner apical spur with row of conical sensilla, more marked than in other species. Cerci one and four-fifths times as long as basal width. Genitalia (Figs 75–77) with cingular apodemes long and strongly curved; rami elongated with exposed portion of cingular and apical penis valves short, subapical ventral process small; epiphallus rectangular with narrow





## Females

Mean	24.20	3.65	3.88	18.05	11.48	2.78	4.12	4.64
Range	21.9–	3.2–	3.4–	16.1–	9.7–	2.4–	3.9–	4.4–
	26.0	4.0	4.4	20.9	12.5	3.0	4.6	4.9
S.D.	1.286	0.215	0.284	1.136	0.769	0.157	0.188	0.157
n	14	15	13	15	15	15	15	13

Sample from China: Hainan Province, Wutoshi.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	21.71	2.95	3.36	16.2	10.33	2.25	4.59	4.81
Range	20.4–	2.7–	3.0–	15.0–	9.5–	2.1–	4.3–	4.1–
	24.1	3.1	3.8	18.0	11.7	2.4	5.1	5.2
S.D.	1.042	0.085	0.210	0.796	0.501	0.095	0.189	0.252
n	23	23	21	23	23	23	23	21

## Females

Mean	26.88	3.71	4.16	20.0	12.32	2.74	4.51	4.82
Range	25.0–	3.4–	3.5–	18.4–	11.2–	2.4–	4.1–	4.5–
	29.7	4.2	4.7	22.2	14.1	3.1	5.0	5.1
S.D.	1.207	0.180	0.267	0.986	0.713	0.168	0.280	0.167
n	18	18	17	18	16	16	16	17

**AFFINITIES.** *O. abruptus* is allied to *O. senegalensis* on the basis of its genitalia and general appearance. However, it may easily be distinguished from any other species by its small size and the distinctive hind wing fascia (Fig. 2).

## MATERIAL EXAMINED

*Gryllus abruptus* Thunberg, lectotype ♂, **China:** 'abruptus  $\alpha$ ' (ZIUU, Uppsala).

In addition to the primary type-material listed above, 191 specimens were examined from the following localities. **Pakistan:** Rawalpindi; Rawalpindi distr., Kallan, 5100 m; Rawalpindi distr., Sangiani. **India:** Mysore St, 12.9 km SE. of Hassan; Pondicherry St, Karikal; Coimbatore, Madras; Coonoor, 1500 m; Madras St, Trichinopoly; Madras St, 12.9 km S. of Yercand; Tinevelly distr., Dohnavur; Coimbatore distr., Siruvani, 510 m, Coimbatore distr., Bolampatti valley; Coimbatore distr., Walayar; Hasanur, Biligirirangan Hills; Alagar Kovil, Madura distr.; Nelliampatti Hills; Travancore, Kottayam; Travancore, Tenmalai, 150–240 m; Coonoor, 1800 m; Bihar, Bhagalpur; Biligirirangan Hills, Dhimban; W. Bengal, Maharajpur; Mysore St, Shimoga distr., Tuppur Forest; Punjab, Murree Hills, Tret; Simla Hills, 1500–2100 m; Punjab, Altoe, 600 m; Simla, 1050–1350 m; Punjab, Gurdaspur; Bengal, Dhub; Jubbulpore. **Sri Lanka:** Jaffna; Malla to Illupallama; Diyatalawa; Hambantota; Colombo; Man distr., Mannar I., 4.8 km NW. of Mannar. **Nepal:** Phewa Tal, nr Pokhara, 750 m; 6.4 km W. of Pokhara, 900 m; Talkot, 1800 m; Arun valley, Tumlingtar, 540–600 m. **Bangladesh:** Dacca. **Burma:** S. Shan states, Kalaw, 1350 m; Upper Burma, 25.8 km on Magwe road, 150 m; Upper Burma, Lashio. **China:** Hainan I., Wutoshi; Hainan I., You Boi; Yergand; Canton, Honan I.; 1 ♀, 'abruptus  $\beta$ ', no data, (ZIUU, Uppsala) (paralectotype of *Gryllus abruptus* Thunberg). **Thailand:** Lop Buri; Udon Thani, 17°25'N, 102°45'E; Chiang Mai; Doi Chiang Dao N, 1200 m.

**DISTRIBUTION** (Fig. 157, and Biogeography section, p. 163). Widely distributed in mainland east Asia.

**BIOLOGY.** *O. abruptus* has at least two generations per year with eggs overwintering from November to April. These hatch to give adults June–July which lay eggs, giving a second generation of adults in August–September (Ahmed *et al.*, 1973). The egg pod is short and fragile, laid in hard soil to a depth of 25–35 mm. There are 18–27 eggs per pod, each about 3.15–4.15 mm long and 0.85–0.95 mm across (Katiyar, 1960). In the laboratory maximum survival rates and fastest development occurred

at 35°C and 8.0% humidity (Khan & Aziz, 1974). Maturation was slower and survival lower in crowded compared to solitary conditions (Khan & Aziz, 1976). The chromosomes have been studied by Asana *et al.* (1939), Dutt (1952; 1955), and Manna (1954). The species is a suitable experimental intermediate host of cestodes parasitic in crows and domestic fowl (Dutt & Sinha, 1961; Dutt & Mehra, 1962). The egg parasite *Scelio aegyptiacus* has been reared from eggs of *O. abruptus* in the laboratory (Ahmed *et al.*, 1973). There are a number of reports of crop damage. Ballard (1921) recorded damage to *Eleusine*, and Chopard & Chatterjee (1937) reported attacks on *Pinus* and *Shorea* seedlings and sandal. *O. abruptus* has also been found on maize and rice (Roffey, 1964; 1965), and is said to feed also on wheat, bajra, jowar, tomato, grain pea, groundnut and other crops (Khan & Aziz, 1974).

**DISCUSSION.** The measurements above indicate that specimens from Hainan are larger with relatively longer tegmina and a larger ratio of femur length to depth than those from Sri Lanka which is the southern limit for this species. It would be of interest to compare these populations with samples from Nepal on the north-west limit of its range. Thunberg's type-material of *Gryllus abruptus* comprises one male, here designated lectotype, and one female, designated paralectotype.

***Oedaleus virgula* (Snellen van Vollenhoven, 1869)**

(Figs 24, 42, 79–82, 162)

*Oedipoda virgula* Snellen van Vollenhoven, 1869: 11. Holotype ♀ [not ♂ as stated by Snellen van Vollenhoven, *op. cit.*], MADAGASCAR (RNH, Leiden) [examined].

*Epacromia inclyta* Walker, 1870: 773. Holotype ♀, MADAGASCAR (BMNH) [examined]. [Synonymized by Uvarov, 1925: 276.]

*Oedaleus (Gastrimargus) madecassus* Saussure, 1884: 115. LECTOTYPE ♀, MADAGASCAR (MHN, Geneva), here designated [examined]. [Synonymized by Uvarov, 1925: 276.]

*Oedaleus (Oedaleus) nigro-fasciatus* var. *virgula* (Snellen van Vollenhoven) Saussure, 1888: 40; Kirby, 1910: 226.

*Oedaleus inclytus* (Walker) Kirby, 1910: 226.

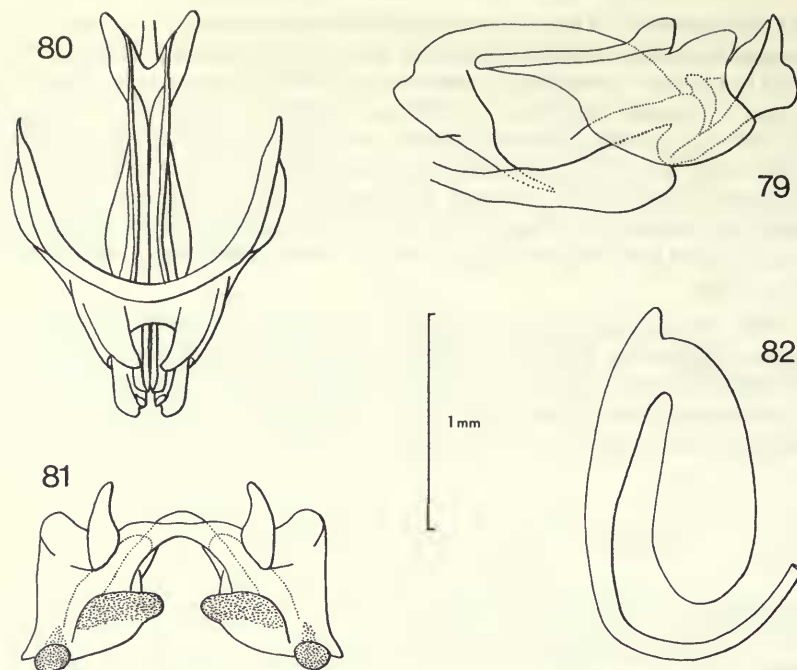
*Oedaleus virgula* (Snellen van Vollenhoven); Kirby, 1910: 226.

*Oedaleus virgulus* (Snellen van Vollenhoven); Dirsh, 1961*b*: 398. [Unjustified emendation.]

**REDESCRIPTION.** ♂. Integument finely rugulose and pitted. Antennae one and a quarter to one and a third times as long as head and pronotum together; flagellum with 22–24 segments. Fastigium of vertex wider than long, anterior width one-third of maximum width, concave with raised margins; frons in profile straight to slightly convex, frontal ridge constricted at vertex and below median ocellus, wider between antennal bases, becoming obsolete ventrally. Eyes nearly one and a half times as deep as wide. Pronotum tectiform, finely punctate; median carina shallowly arcuate, hind margin acutangular to obtusangular. Tegmen surpassing hind knees by two-fifths to one-half of hind femur length. Hind tibia with 11 inner and outer spines; inner apical spurs twice as long as outer, apical tarsal segment twice length of claw, arolium more than half claw length. Cerci about two and a quarter times as long as basal width. Genitalia (Figs 79–81): cingular apodemes slender, rami moderate length; cingular and apical penis valves short; subapical ventral process large; epiphallus almost rectangular with thin bridge; inner lobes of lophi strongly transverse, two and a half times as wide as outer lobes; anterior projections large, rounded; posterior projections small, sharply acutangular.

General coloration variable, greenish or brownish, with lighter markings on frons, genae, pronotum, tegmina and hind femora. Pronotal X-marking (Fig. 24) sometimes obsolescent. Tegmen infusate in basal half with four pale transverse bands extending from costal margin; first band one-sixth along from base, reaching second cubitus, second band one-third along, reaching first or second cubitus, third band reaching and following *Culb* as a distinct oblique white stripe; fourth band two-thirds along, reaching posterior medial vein; apical third of wing mottled with brown and transparent cells. Hind wing without fascia or with very pale indistinct fascia barely visible posterior to second anal vein; basal area pale yellow. Hind femur with three variable transverse dark markings on external and internal upper marginal areas, extending obliquely across external and internal medial areas, sometimes obsolescent; ventral surface of femur straw-coloured, hind knee brown. Hind tibia with dark basal ring, subbasal pale area, otherwise pale blue-grey.

♀. Ventral ovipositor valves (Fig. 42) blunt, heavily sclerotized, exterior lateral surface almost straight; basivalvular sclerite coarsely rugose. Spermatheca (Fig. 82) with apical diverticulum elongate and short blunt sub-apical diverticulum.



Figs 79–82 *O. virgula*, genitalia. 79, endophallus and cingulum, lateral view; 80, same, dorsal view; 81, epiphallus; 82, spermatheca.

#### MEASUREMENTS

Sample from Madagascar: various localities.

#### Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25.87	3.43	4.33	19.39	12.53	2.97	4.22	4.48
Range	22.1–28.7	3.2–3.8	3.6–5.0	16.4–21.5	11.1–13.9	2.6–3.2	3.9–4.5	4.0–4.8
S.D.	1.829	0.139	0.354	1.512	0.732	0.141	0.182	0.190
n	21	21	21	21	17	17	17	21

#### Females

Mean	34.58	4.77	5.90	25.89	16.0	3.84	4.18	4.4
Range	29.7–38.4	4.3–5.2	4.9–7.0	21.8–28.9	14.1–18.3	2.7–4.5	3.8–5.1	3.9–4.7
S.D.	2.624	0.249	0.476	1.978	1.226	0.307	0.255	0.225
n	33	31	34	34	32	31	31	33

AFFINITIES. *O. virgula* belongs to the same species-group as *O. senegalensis* and *O. nigrofasciatus* on the basis of the pale hind tibia and underside of the hind femur, and the close similarity of the genitalia, particularly the epiphallus (Fig. 81). It is, however, easily distinguished from all the other species of the group by the absence of a distinct wing band.



## MATERIAL EXAMINED

*Oedipoda virgula* Snellen van Vollenhoven, holotype ♂, Madagascar: no further data (RNH, Leiden). *Oedaleus (Gastrimargus) madecassus* Saussure, lectotype ♀, Madagascar: no further data (MHN, Geneva). *Epacromia inclyta* Walker, holotype ♀, Madagascar: no further data.

**Madagascar:** 1 ♂, 2 ♀, no further data; 1 ♀, Majunga s. l., 25.ii–3.iii.1968 (Guichard); 1 ♂, 4 ♀, Glorieuses Is., 21.xi.1952 (Brown); 2 ♀, Ejeda, Betioky, Tulear, 27.i.1928 (Zolotarevsky); 1 ♂, 3 ♀, same data, 1.ii.1928; 3 ♀, same data, 21.ii.1928; 5 ♀, same data, 16.ii.1928; 2 ♀, same data, 5.v.1928; 1 ♂, 2 ♀, Sakamena, Betioky, 15.v.1928 (Zolotarevsky); 4 ♀, Ankazoabo, Tulear, 7.vi.1927 (Zolotarevsky); 1 ♂, Namsana, Tananarive, 18.ix.1928 (Zolotarevsky); 3 ♀, Ankililoaka, Tulear, 26.v.1927 (Zolotarevsky); 1 ♂, Nossi Bé, xi.1952 (Brown); 1 ♂, Ambohimandry, 30.viii.1913 (Beck); 1 ♀, Tsiafakomba, Adriba Isibefe (Beck); 5 ♂, 3 ♀, Antanemora, 300 m, xi–xii.1959 (Ross) (CAS, San Francisco); 3 ♂, 4 ♀, Zombitsy forest, nr Sakaraha, 650 m, 16.xii.1959 (Ross) (CAS, San Francisco); 1 ♂, 1 ♀, Tananarive, 5.xii.1959 (Ross) (CAS, San Francisco); 8 ♂, 1 ♀, same data, x.1949 (CAS, San Francisco); 2 ♂, Amboasary, Ft Dauphin dist., 18.iv.1969 (Hardy) (DATS, Pretoria); 2 ♂, 1 ♀, Tananarive, iii.1918 (Lamberton) (ANS, Philadelphia); 1 ♀, same data, ii.1918 (ANS, Philadelphia); 1 ♀, Behanka, Betioky, Tulear, 27.i.1928 (Zolotarevsky). **Aldabra:** 1 ♂, 1 ♀, Ans Mais, 22.iv.1977 (Waloff) (COPR, London). **Zanzibar:** 1 ♀, no data (Hildebrandt) (MNHU, Berlin). **South Africa:** 1 ♀, Cape of Good Hope, 1820 (Delalande) (MNHN, Paris) [almost certainly mislabelled].

**DISTRIBUTION** (Fig. 162, and Biogeography section, p. 163). Widely distributed and common within Madagascar, and newly recorded from Zanzibar and Aldabra. There is one specimen purporting to be from South Africa, but this is presumably mislabelled.

**BIOLOGY.** Little is known of the biology of this species. The following information is derived from Descamps & Wintrebort (1966). One egg pod was measured and found to be  $57.5 \times 5.0$  mm, slightly bent, with 30 eggs arranged in 11 rows of 2–4 eggs each. The individual eggs are about  $4.1 \times 1.0$  mm and have a chorionic sculpture composed of irregular dots forming indistinct rows, with neighbouring dots sometimes joined by fine lines. In the cool season incubation lasts at least two months. The sixth instar may last a month. Nymphs are particularly common in September, November, March, and April. There are three or possibly four generations per year with an apparent movement of adults southward at the end of the hot season. Three species of *Scelio* were recorded as egg parasites.

**DISCUSSION.** The emendation of the specific name *virgula* to *virgulus* (Dirsh, 1961*b*) is here rejected because *virgula*, meaning a wand, is a feminine noun in apposition and not an adjective.

Saussure's description of *O. madecassus* was based on material in his own and Brunner's collections. The single male of this species in the MHN, Geneva, bears the following labels: 'Madagascar M. H. de S.' 'Oedaleus madecassus Sss. Madag.' This specimen is here designated as the lectotype. The status of material in the NM, Vienna, is not clear and accordingly no paralectotypes have been designated.

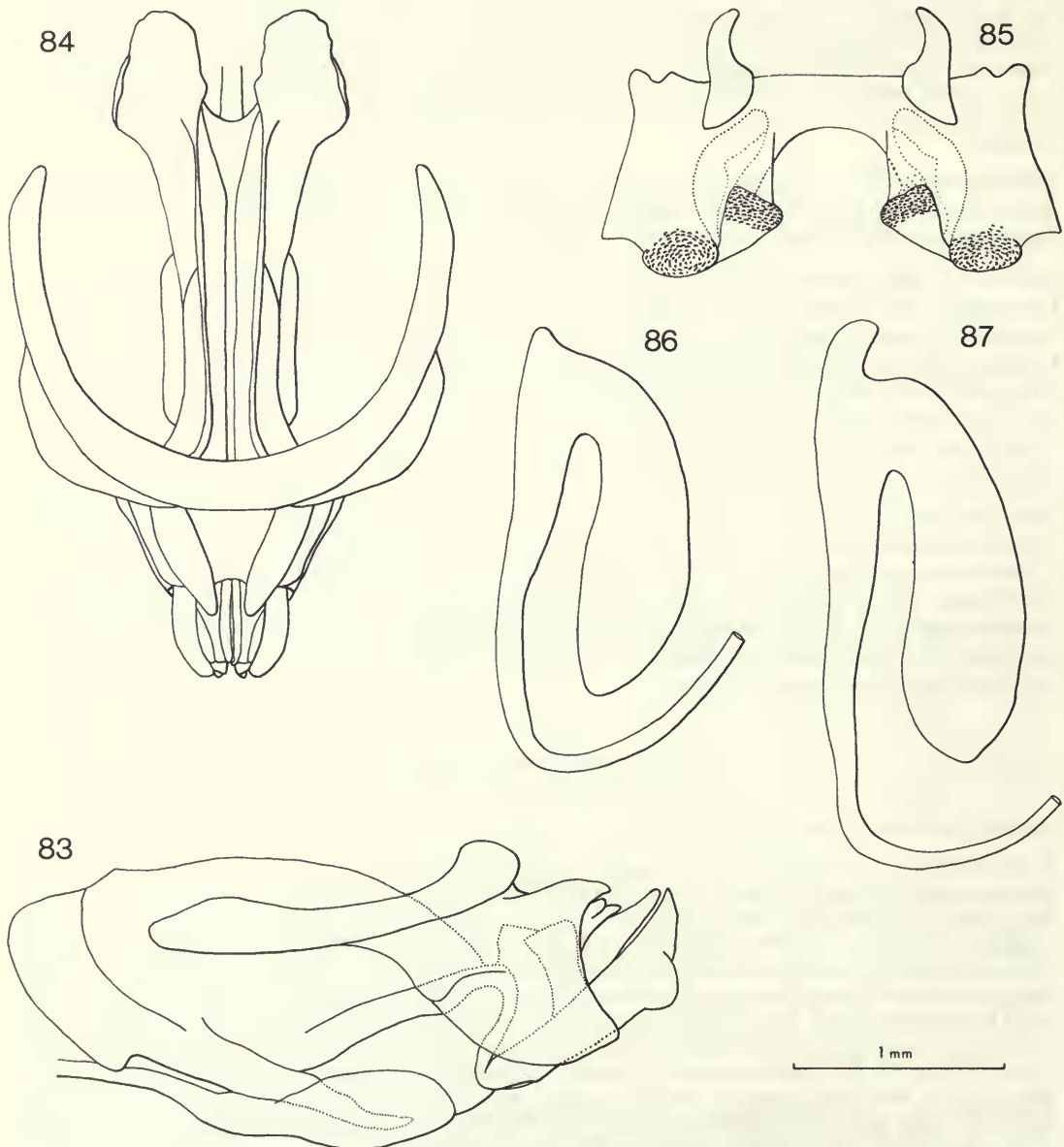
***Oedaleus johnstoni* Uvarov, 1941**  
(Figs 14, 19, 43, 83–87, 155)

*Oedaleus johnstoni* Uvarov, 1941: 58. Holotype ♂, SUDAN: Khartoum (BMNH) [examined].

**REDESCRIPTION.** ♂. Integument finely rugulose. Antennae about one and two-fifths length of head and pronotum together; flagellum usually 22-segmented. Fastigium wider than long, concave, with raised margins, narrowing to half maximum width anteriorly. Frons in profile flat or slightly convex; frontal ridge slightly expanded at ocellus. Eyes barely deeper than wide. Pronotum low tectiform to saddle-shaped, finely rugulose, pitted, and with well-marked sulci; median carina low and cut by posterior sulcus. Hind margin of pronotum smoothly rounded. Tegmen surpassing hind knees by about one-third of femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a quarter times as long as claw; arolium about one-third length of claw. Cerci almost twice as long as basal width. Genitalia (Figs 83–85): circular apodemes long and strongly curved, zygoma only slightly thickened; rami long; circular and apical penis valves short. Apical penis valves with acute apices and tumulus-shaped subapical ventral process. Epiphallus long and broad with deeply arched bridge; outer lobes of lophi wider than inner lobes; anterior and posterior projections large and acutangular.

General coloration mottled, variable, from dark brown to sandy or greenish. Head mainly light brown, sometimes with frons and vertex green. Lateral surface of pronotum and thorax mottled with variable light and

dark patches. Pronotum sometimes entirely green on dorsum of prozona and metazona but laterally on metazona only. Tegmen mottled with two indistinct variable transverse bands in basal two-thirds, apex with some dark speckling. Hind wing fascia (Fig. 14) incomplete, not reaching posterior margin and not passing 2*A* anteriorly; basal area pale yellow. Outer surface of hind femur with three indistinct oblique dark bands, inner surface with some bands visible in upper-marginal area but medial area clear straw-coloured, with orange sulci in chevron pattern, lower marginal area bright orange. Hind knees with internal surface and external crescent black. Hind tibia bright orange internally, orange-yellow externally.



**Figs 83–87** *O. johnstoni*, genitalia. 83, endophallus and cingulum, lateral view; 84, same, dorsal view; 85, epiphallus; 86, 87, spermatheca, showing variation.

♀. Pronotum more rugose. Ventral ovipositor valves (Fig. 43) barely longer than wide, slightly excavated laterally; basivalvular sclerite sclerotized and with rugose warts. Spermatheca (Figs 86, 87) elongate with short, variable subapical diverticulum.

## MEASUREMENTS

Sample from Mali; Adrar des Iforhas.

Males								
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur width	FL/FD	TL/PL
Mean	30.18	4.88	4.87	21.90	13.80	3.88	3.74	4.56
Range	26.3–	4.5–	4.2–	18.4–	12.6–	3.1–	3.5–	3.9–
	35.4	5.3	5.6	25.9	17.3	4.4	4.2	5.3
S.D.	2.267	0.223	0.357	1.864	3.126	0.384	0.211	0.373
n	14	19	19	14	19	19	19	14

Females								
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur width	FL/FD	TL/PL
Mean	40.09	6.67	6.38	29.03	18.58	4.79	3.89	4.55
Range	36.75–	6.1–	5.5–	26.0–	17.0–	4.1–	3.6–	4.0
	45.5	7.6	7.7	32.8	21.0	5.7	4.2	4.8
S.D.	2.69	0.425	0.633	1.934	1.269	0.474	0.188	0.23
n	20	20	21	20	21	21	21	20

**AFFINITIES.** *O. johnstoni* is most closely allied to *O. senegalensis* and *O. nigeriensis*, having the rounded pronotal hind margin of the former and the orange-red hind tibiae and under surface of the hind femur reminiscent of the latter. It is, however, quite distinct, being more heavily built and having a lighter, less distinct pattern than either of these species.

## MATERIAL EXAMINED

*Oedaleus johnstoni* Uvarov, holotype ♂, **Sudan**: Khartoum, 25.ix.1924 (*Johnston*) (BMNH).

**Mauritania**: 5 ♂, 4 ♀, 17° 12' N, 13° 58' W, light trap, 19.ix.1973 (*Popov*); 2 ♂, 1 ♀, Aioun, 16° 40' N, 9° 31' W, 10.x.1961 (*Popov*). **Mali**: 4 ♂, 2 ♀, Adrar Mts, nr Tabankort, 7.ix.1959 (*Popov*); 1 ♀, Pèhé, 40 km N. of Dioura, 16.x.1956 (*Davey*); 2 ♂, 1 ♀, Tillemsi Valley, road from Kidal to Tin-Essakou, 29.ix.1974 (*Ritchie*) (COPR, London); 17 ♂, 20 ♀, Adrar de Iforhas, Oued Edjerer, 30.ix.1974 (*Ritchie*) (COPR, London). **Niger**: 1 ♂, 30 km E. of Agadez, 20.ix.1965 (*Popov*); 1 ♀, Gall-Abangharit, 10.xii.1960 (*Popov*); 2 ♂, 5 ♀, Abangharit, 12–19.ix.1965 (*Popov*); 1 ♀, Aïr, 100 km N. of Agadez towards In Guezzam, 25.viii.1967. **Sudan**: 4 ♂, 1 ♀, Khartoum, 25.ix.1924 (*Johnston*) (paratypes of *Oedaleus johnstoni* Uvarov); 1 ♀, Khartoum (*King*) (paratype of *O. johnstoni*); 3 ♂, 1 ♀, Khartoum, 20.ix.1970, 1 ♂, 4 ♀, Kassala, 3.x.1926 (*Johnston*) (paratypes of *O. johnstoni*); 5 ♀, Aroma, short grass, 30.ix.1926 (*Johnston*) (paratypes of *O. johnstoni*); 1 ♂, 4 ♀, Aroma, dry grass, 3.x.1926 (*Johnston*) (paratypes of *O. johnstoni*); 1 ♂, 4 ♀, no further data (paratypes of *O. johnstoni*); 6 ♂, N. Darfur, clay wadi, at light, 9.ix.1934 (*Darling*); 1 ♀, N. Darfur, Jebel Jeiga, 24.ix.1934 (*Darling*); 1 ♀, Wad Medani, at light, ix.1927 (*Johnston*); 1 ♀, Barakat, 10.x.1974 (*Haggis*) (COPR, London); 1 ♀, Barakat, 14.x.1974 (*Haggis*) (COPR, London). **Ethiopia**: 1 ♂, Harerge pr., Melka Werer, Inst. Agr. Res., 14.5 km ENE. of station, 30.ix.1975 (*Jago*) (MA, Addis Ababa). **Oman**: 1 ♂, Al Khaburah, 22.x.1970 (*Tunstall*) (COPR, London).

**DISTRIBUTION** (Fig. 155, and Biogeography section, p. 162). Occurs in a thin band across the northern Sahel from Mauritania to Ethiopia (*Jago*, 1977), and there is one known specimen from Oman, a new record which needs confirmation. An erroneous record from Senegal by Roy (1962: 130) was later identified as *Oedaleus nigeriensis* Uvarov (Roy, 1965: 616).

**BIOLOGY.** Little is known of the biology of this species. Joyce (1952) recorded it from sandstone and serpentine outcrops in east-central Sudan, and regarded it as the dominant species in sandy areas of



the Gash river delta (200–300 mm annual rainfall) and the clay plains of the northern Gezira (150–200 mm rainfall). Adults were found from August to November with peak numbers in August and September. Hoppers occurred between July and October and mature females from August. Joyce postulated two annual generations, with the dry season passed in the egg stage in dry soils. There are records of damage to millet (Joyce, 1952) and to cotton (Joyce, 1956) but such damage is probably rare and of small extent.

*O. johnstoni* normally occurs in low densities but very high density populations have been reported. Dr R. Skaf (pers. comm.) observed bands of fourth and fifth instar hoppers at a density of 100/m<sup>2</sup> marching westward downwind in the Oued Edjerer (18°26'N 02°02'E) in NE. Mali on 20.viii.1974. The hoppers collected exhibited pronounced black and brown coloration like that of high density hoppers of *O. senegalensis*, and small numbers of adult *O. senegalensis* were mixed among them. On 30.ix.1974 I visited the locality and found adults only at about 1 per 2–3 m<sup>2</sup>. The decline in numbers over five weeks may be attributed to dispersal of adults by flight since the species is often caught at light some distance from areas where it can be found by day. *O. johnstoni* is the dominant grasshopper species in the flat, gravelly silt oueds flowing into the Tillemsi valley from the rocky outcrops of the Adrar des Iforhas, and its coloration is well matched to that of the extensive patches of bare soil on which it rests. The sparse vegetation consists of low hummocks of *Tribulus*, *Euphorbia*, *Indigofera*, *Farsetia*, and *Heliotropium* with *Aristida* and *Panicum turgidum*. The insects fly readily when first disturbed but land and hide within the clumps of vegetation and are then difficult to flush a second time.

Adult specimens possess a pronotal gland similar to that found in *O. senegalensis* but no hoppers were available for dissection. The ovaries of seven adult females were dissected and the mean number of ovarioles per ovary was found to be 26.8 with a range from 23 to 31.

### *Oedaleus nigeriensis* Uvarov, 1926

(Figs 10, 20, 39, 88–91, 161)

*Oedaleus nigeriensis* Uvarov, 1926: 437. Holotype ♂, NIGERIA (BMNH) [examined].

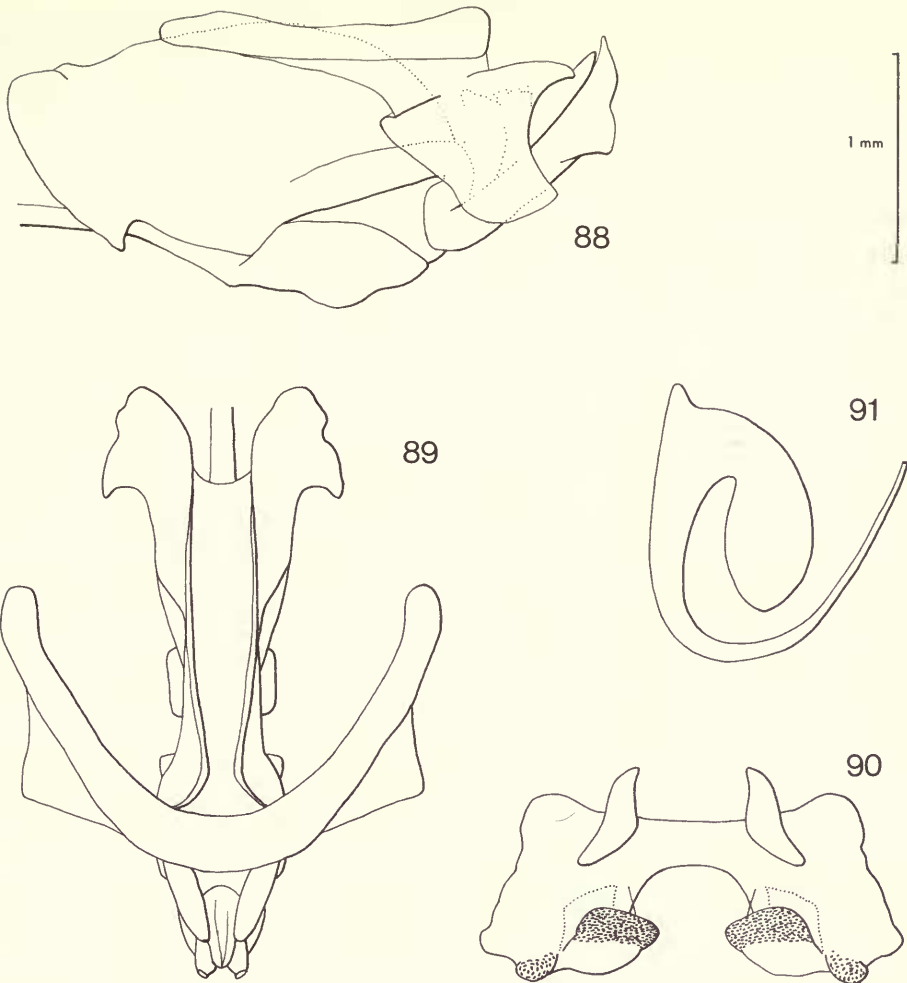
*Oedaleus senegalensis* (Krauss) var. *b.* Saussure, 1884: 117; Bolivar, 1908: 102.

*Oedaleus cephalotes* Uvarov, 1934: 606. Holotype ♀, ETHIOPIA (BMNH) [examined]. **Syn. n.**

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and three-fifths times as long as head and pronotum together, flagellum with twenty segments. Fastigium longer than wide, shallowly concave, narrowing to two-fifths of maximum width anteriorly; frons in profile convex; frontal ridge barely constricted below median ocellus, becoming obsolete ventrally. Eyes one and two-fifths as deep as wide. Pronotum low tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin obtusangular to rounded obtusangular. Tegmen surpassing folded hind knees by two-fifths to one-half of hind femur length. Hind tibia with 10–11 inner and 8–10 outer spines; inner apical spurs one and three-fifths as long as outer; apical tarsal segment two and one-fifth times as long as claw; arolium three-fifths length of claw. Cerci barely more than twice as long as basal width. Genitalia (Figs 88–90): cingular apodemes short and moderately curved; rami elongate dorsally; exposed section of cingular and apical penis valves short; subapical ventral process rectangular; epiphallus trapezoidal, bridge narrow; inner lobes of lophi twice as wide as outer lobes; anterior projections large and rounded; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on vertex, frons, genae, pronotum and dorsal surface of folded tegmina and hind femora. Tegmen infuscate brown in basal two-thirds with irregular pale transverse bands one-third and one-half along from base; apical one-third clear with variable brown patches. Hind wing fascia (Fig. 10) broadly interrupted between first cubitus and second anal vein, reaching or nearly reaching to hind margin posteriorly; wing tip infumate, basal area pale yellow. Hind femur with three indistinct dark variable oblique transverse bands on outer and inner upper marginal areas and outer medial area; inner surface light reddish brown becoming pale red ventrally; hind knees dark brown; hind tibiae with dark basal ring and subbasal pale area, otherwise light red.

♀. Ventral ovipositor valves (Fig. 39) long, well sclerotized, outer margin almost straight. Apical diverticulum of spermatheca (Fig. 91) with short subapical diverticulum.



**Figs 88–91** *O. nigeriensis*, genitalia. 88, endophallus and cingulum, lateral view; 89, same, dorsal view; 90, epiphallus; 91, spermatheca.

MEASUREMENTS

Sample from Zambia: Musosa, xi–xii.40 [beginning of rainy season] (*H. J. Bredo*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23.99	3.33	3.725	17.75	11.44	2.87	3.98	4.73
Range	22.1–25.8	3.1–3.7	3.3–4.1	16.7–18.7	10.4–12.6	2.7–3.0	3.6–4.4	4.3–5.3
S.D.	0.999	0.152	0.216	0.661	0.661	0.071	0.200	0.222
n	16	17	16	16	17	17	17	15

## Females

Mean	29.99	4.47	4.78	22.22	13.96	3.64	3.83	4.66
Range	26.5–	3.9–	4.2–	19.6–	12.0–	3.1–	3.6–	4.2–
	33.5–	5.0	5.3	25.5	15.4	4.0	4.1	5.2
S.D.	1.558	0.223	0.275	1.331	0.819	0.165	0.128	0.235
n	20	20	20	20	20	20	20	20

Sample from Zambia: Musosa, iv–v.41 [end of rainy season] (*H. J. Bredo*).

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	29.05	4.33	4.57	21.36	14.82	3.39	4.37	4.69
Range	27.0–	4.1–	4.2–	20.1–	14.4–	3.0–	4.1–	4.2–
	30.4	4.7	5.1	22.4	15.5	3.7	4.7	5.1
S.D.	1.051	0.186	0.261	0.790	0.530	0.204	0.172	0.231
n	10	10	10	10	9	10	9	10

## Females

Mean	36.49	5.78	5.71	26.57	18.42	4.31	4.28	4.67
Range	34.7–	3.5–	5.2–	25.4–	16.8–	4.2–	4.0–	4.4–
	37.8	6.2	6.2	27.8	20.2	4.5	4.8	5.0
S.D.	1.286	0.239	0.417	0.896	1.323	0.134	0.313	0.22
n	5	5	5	5	5	5	5	5

Sample from Ethiopia: Nefasit, 28.viii.68 (*J. Tunstall*).

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23.62	3.72	3.9	17.04	12.54	3.14	3.99	4.38
Range	22.3–	3.4–	3.6–	16.1–	11.5–	2.9–	3.7–	3.9–
	26.1	4.2	4.3	19.1	13.5	3.4	4.2	4.70
S.D.	1.267	0.210	0.227	0.937	0.592	0.148	0.156	0.22
n	11	11	11	11	11	11	11	11

## Females

Mean	32.24	5.36	5.24	22.66	16.69	4.07	4.1	4.33
Range	28.9–	4.8–	4.5–	20.8–	14.4–	3.6–	3.8–	4.1–
	35.9	5.7	5.8	24.9	19.1	4.4	4.4	4.7
S.D.	1.905	0.279	0.369	1.088	1.141	0.224	0.177	0.176
n	12	12	12	12	12	12	12	12

AFFINITIES. *O. nigeriensis* is a member of the same group of species as *O. senegalensis*, characterized by the possession of large transverse inner lobes to the epiphallic lophi. It is most closely allied to *O. carvalhoi* from which it may be separated by the principal characters listed under that species (p. 117).

## MATERIAL EXAMINED

*Oedaleus nigeriensis* Uvarov, holotype ♂, **Nigeria**: Azare, vii.1925 (*Lloyd*) (BMNH). *Oedaleus cephalotes* Uvarov, holotype ♀, **Ethiopia**: Muger Valley, c. 5500' [1600 m], 28–29.xii.1926 (*Scott*) (BMNH).



In addition to the holotypes, 787 specimens were examined from the following localities. **Senegal:** Bambe; Dakar; Dakar, Cape Manuel; Yoff; Mt Rolland; Diebering; Thies. **Mauritania:** Néma; Selibaby area. **Mali:** Bamako; Kara, Macina; Sangha Village; 2.4 km E. of Sangha; Klela; Gourima, nr Darou; Dogo; Nioudji. **Upper Volta:** Ouagadougou. **Ghana:** Volta Region, Nkwanta to Chiare; N. region, 8 km S. of Lepusi, 51.5 km S. of Yendi; Nakpanduri, Gambaga Scarp; Navrongo; N. region, Damongo. **Togo:** Mangu; Kete Kratje. **Niger:** Niamey to Tillabery, 35 km from Niamey; Elewayen, agric. station; Danga village, nr Ouallam. **Nigeria:** 2 ♂, 1 ♀, Azare, vii.1925 (*Lloyd*) (paratypes of *Oedaleus nigeriensis* Uvarov); Ibadan, Ife University campus; Kalkala; Ngornu, Bornu; Potiskum; Sherifuri, nr Azare; Ngala; Kerenua; Maiduguri; Dikwa; Shagisnu; Wurge; Birnin Kudu; Maiduguri to Bama road; km 35–37, Mongonu to Maiduguri road; 8.9 km W. of Gulumba; 2.5 km N. of Debele village; Lamurde hills; Zaria; Zaria, Samaru; 50 km S. of Bama; 45 km SE. of Maiduguri; Bauchi, air strip; Maska, fish farm; nr Yola; 96.6 km along Kaduna to Tegina road; Shika, I.A.R. farm; nr Difa, Gombe area; nr Deba Habe; Zambuk, nr Gombe; nr Bilbis turn-off, on Zaria to Chafe road. **Cameroon:** Gore; Kuni; Kaitia; Sogane to Gore; Middle Adamaua, 300–500 m, v. Garua und Rei Buba, n. Monti; Garua; Satsche. **Congo:** environs of Brazzaville. **Central African Empire:** Batangafo, Ubangi to Shari. **Zaire:** Mahagi Port; Kawa, L. Albert; Ekibondo, between Niangara and Dungu, Uele, 795 m; Kasenyi, L. Albert, 630 m. **Angola:** E. region; Moxico distr., Villa Luzo, 900 m; Moxico Pr., Villa Luzo; Moxico distr., R. Lumeji; 8 km NE. of Negola. **Zambia:** Lusaka distr.; Lusaka distr., nr Kipopo; Ndola; Livingstone; 30 km outside Kitwe; Musosa. **Tanzania:** Kondo; Old Shinyanga; Ushiroambo road, 16 km W. of Kahama; Mkwemi, 35.4 km W. of Kahama; Central Rukwa, side of W. escarpment; C. Rukwa, Kapombo; C. Rukwa, Kafukola; Nakachese, Rukwa rift; Momba R., Rukwa rift. **Uganda:** Butiaba, L. Albert, Unyoro, 624 m; Lango, Kigaa (Agaya); Lango; Bugwere; W. Nile distr.; Dokolo; Moroto; Karamoja, Kotido; S. Karamoja, Madi Opei; Soroti; Teso; Adachal; Butiaba; Kamuli, Busoga; Bukumi, L. Albert; Sukh plains, nr Nepal Pass; Buruli; Chiawante, Lango; Mbale. **Kenya:** Kindaruma, 3.2 km N. of bridge across Tana R., 00°47.5'S, 37°39.5'E, 1070 m; Makindu; 41 km N. of Kitui, 01°08.5'S, 37°44'E; Athi R. crossing, 25.8 km NNE. of Kibwezi, 420 m; Sumba Springs; Murinduko hill (top), 4.8 km S. of Embu town, 00°35'S, 37°27'E, 1300 m, game area owned by Taita Hills Lodges, 03°32'S, 38°14'E, 900 m; Kiitoo Coffee Estate, 00°58'S, 37°17'E, 1560 m. **Sudan:** Imatong Mts, Lorno, 810 m; Imatong Mts, Molongori, 750 m; Bahr el Ghazal, 16 km W. of Rumbeck, on Wau to Rumbeck Road; Opari; Talodi; Gedaref, M.C.P.S.; Kerrippi. **Ethiopia:** Nefasit; Batie; Harar; Macalle; Addis Ababa to Debra Marcos road, Abbai gorge, about 2100 m; Eritraea, Elabaret; 1 ♀, plains NW. of L. Zwai, 1650–1950 m, 31.x.–1.xi.1926 (*Scott*) (paratype of *Oedaleus cephalotes* Uvarov); 1 ♂, no data (paratype of *O. cephalotes* Uvarov); Shewa Province, Mojo to Shashamene road, km 104.7, L. Shala bird sanctuary; 1 ♀, Wambar Mariam, Mt Zuquala, 2100 m, 28.x.1926 (*Scott*) (paratype of *O. cephalotes* Uvarov); Tembine distr., Avergalle area. **Comoro Is.:** 1 ♂, Grand Comoro, coast, 3.vii.1903 (*Voeltzkow*) (MNHU, Berlin).

**DISTRIBUTION** (Fig. 161, and Biogeography section, p. 163). Widely distributed in moist savannah and woodland from Senegal to Ethiopia and southwards through central Africa to the southern limits of the *Brachystegia* woodland. Newly recorded from Grand Comoro I.

**BIOLOGY.** The life history and ecology of *O. nigeriensis* were studied in Nigeria by Golding (1948) who stated that there were probably three generations in the south but only one in the north. In West Africa as a whole adults are to be found from April through to January. In Tanzania Robertson & Chapman (1962) made an ecological study which suggested that there were two generations between January and July, but they were unable to decide whether the species survived the dry season in the egg or adult stage, or in both. They presented evidence suggesting that young adults leave the grasslands and enter the woodland to feed or oviposit. In Cameroon Descamps (1953) postulated two generations with an embryonic diapause. The egg pod and eggs have been described by Chapman & Robertson (1958) who found 12–42 eggs per pod. The species has been recorded damaging maize (Descamps, 1954; Mallamaire, 1956), *Pennisetum* and *Eleusine* millet (Risbec, 1950; Golding, 1946; Libby, 1968; Harris, 1949), rice seedlings (Risbec & Mallamaire, 1949), groundnuts and sweet potato (Risbec, 1950) and tobacco and yams (Libby, 1968).

**DISCUSSION.** The measurements of specimens from Musosa, Zambia show the remarkable change in size exhibited by the species over six months. The ranges of measurements from the two samples barely overlap, and are clearly significantly different. Less obviously the ratio of femur length to depth is also significantly different as indicated by a 't' test ( $P < 0.001$  ♂,  $< 0.1$  ♀). It is not clear whether the two samples at either end of the rainy season represent two different generations of the same population or rather a migration into the locality of a population from elsewhere between the

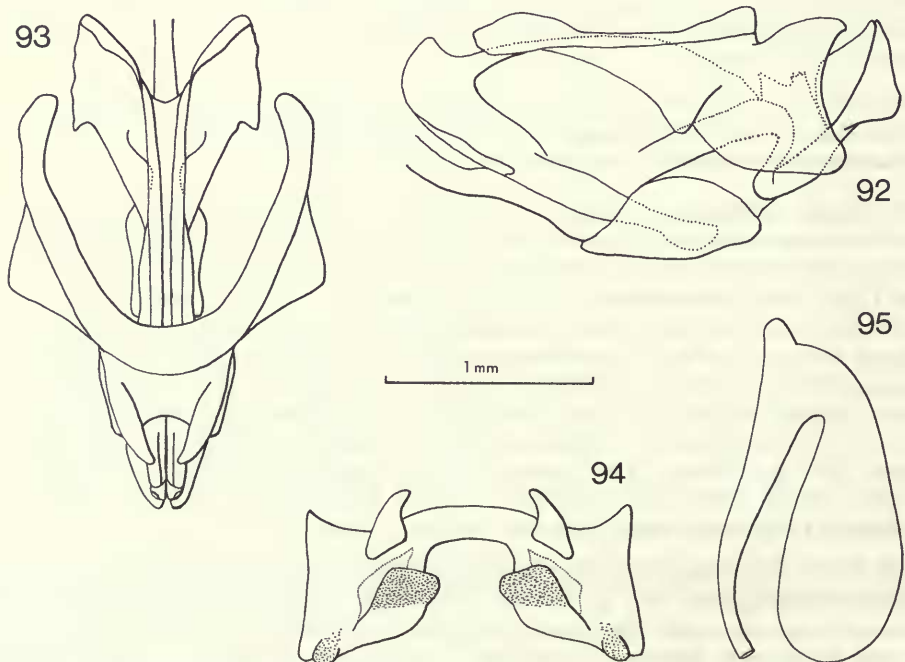
two sampling periods. For present purposes, however, these figures provide an indication of the range of size within the species. Series from Ethiopia and Tanzania fall within the extremes recorded from Zambia. Material from Ethiopia was originally named as a separate species, *O. cephalotes*, by Uvarov (1934) at a time when relatively little material of *O. nigriensis* was known, and that only from Nigeria. It has now become clear that the same species is to be found without a break right across Africa. The original description of *O. cephalotes* made no comparison with material of previously described *Oedaleus* species.

***Oedaleus carvalhoi* Bolívar, 1889**  
(Figs 15, 23, 44, 92–95, 152)

*Oedaleus carvalhoi* Bolívar, 1889: 103. Syntypes (?) ♂♀, MOZAMBIQUE: Lourenço Marques [Maputo] (*Monteiro*) (lost). NEOTYPE ♂, MOZAMBIQUE (ANS, Philadelphia), here designated [examined].

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae barely longer than head and pronotum together, flagellum with 21 segments. Fastigium of vertex longer than wide, concave, narrowing to less than half of its maximum width anteriorly, with distinct lateral carinae; frons in profile straight, frontal ridge barely constricted below median ocellus, becoming obsolete ventrally. Eyes one and a third times as deep as wide. Pronotum tectiform, median carina arcuate, not intersected by posterior sulcus; hind margin forming an obtuse angle with concave sides (Fig. 23). Tegmen surpassing hind knees by one-quarter to one-eighth of hind femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times outer; apical tarsal segment one and three-quarter times claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs 92–94): cingular apodemes long and incurved; rami elongate with short cingular and apical penis valves; subapical ventral process large, rounded; epiphallus rectangular with narrow bridge, inner lobes of lophi strongly transverse, more than twice width of outer lobes; anterior projections large, acute; posterior projections small, rounded.

General coloration variable, brown, with lighter brown or green markings on frons, vertex, genae, pronotum and dorsal surface of folded tegmina. Pale X-marking of pronotum often surrounded by longitudinal dark brown area. Tegmen matt brown in basal half with two irregular pale transverse bands one-third and one-half distance from base, sometimes obsolete; apical half becoming clear with irregular brown markings. Hind wing



Figs 92–95 *O. carvalhoi*, genitalia. 92, endophallus and cingulum, lateral view; 93, same, dorsal view; 94, epiphallus; 95, spermatheca.

fascia (Fig. 15) interrupted between first cubitus and second anal vein, reaching or almost reaching hind margin of wing; apex of wing infumate, basal area pale yellow. Hind femur with three indistinct variable oblique transverse dark bands on external medial and upper marginal areas; inner surface brown, indistinctly mottled, ventral surface dull brown; hind knees dark brown, hind tibiae with dark basal ring and pale subbasal area, otherwise dull brown.

♀. Hind wings sometimes barely exceeding folded hind knees. Ventral ovipositor valves short, well sclerotized, hardly incurved externo-laterally (Fig. 44). Spermatheca (Fig. 95) with short subapical diverticulum.

## MEASUREMENTS

Sample from South Africa: Transvaal, Louis Trichardt.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23.32	3.47	4.31	16.85	12.21	3.01	4.06	3.92
Range	21.5–25.2	3.0–4.6	3.9–5.1	15.4–18.3	10.3–14.1	2.7–3.5	3.7–4.4	3.6–4.3
S.D.	1.131	0.333	0.301	0.864	0.948	0.199	0.211	0.181
n	20	20	20	20	20	20	20	20

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26.88	4.69	5.42	18.77	14.26	3.65	3.91	3.47
Range	24.8–28.7	4.5–5.0	5.1–5.9	17.0–19.7	13.5–15.1	3.4–3.9	3.6–4.2	3.1–3.7
S.D.	1.032	0.139	0.204	0.781	0.482	0.149	0.173	0.172
n	15	15	15	15	15	15	15	15

**AFFINITIES.** *O. carvalhoi* is most closely allied to *O. nigriensis* from which it differs by the following principal characters. Tibiae and ventral surface of hind femur pale straw-coloured, not red. Pronotum with finer cross-shaped marking and more pointed hind margin (Figs 23, 20). Tegmina and wings shorter in relation to body size and pronotum length (compare TL/PL ratios given for both species).

## MATERIAL EXAMINED

*Oedaleus carvalhoi* Bolívar, neotype ♂, **Mozambique:** Lourenço Marques [Maputo], 12.vii.1910 (ANS, Philadelphia).

In addition to the neotype, 263 specimens were examined from the following localities. **Mozambique:** 35 km NE. of Chitengo, Gorongoza; 9.7 km E. of Vila Machado; Namaacha; 10 km E. of Marraguere; Missão de S. Roque, Maputo; Massinga; Zambezi R., Sena Sugar Estate; Beira, Milange; Beira, Luabo; Beira, Salone forest; Muccheve; Delagoa Bay, Inhaca I.; Buzi R.; Delagoa Bay. **Zambia:** Livingstone. **Zimbabwe:** West Nicholson, Masase; Dotts Drift, Chisumbanje, Lower Sabi; Mt Selinda, 1350 m; Bizana distr., Pondoland E.; 22.5 km NW. of Gwanda, Old Gwanda road, 1050 m; Shangani, de Beers Ranch; Matopo Hills; Odzi distr., Selukwe, 1500 m; Zimbabwe, nr Fort Victoria; Victoria Falls, 900 m. **Botswana:** Siane, Chobe. **Namibia:** Gobiswater Farm, 19.3 km N. of Grootfontein, 19°23'S, 18°08'E, c. 1400 m. **South Africa:** Transvaal, Zoutpansberg, 9.7 km NNE. of Louis Trichardt; T., Louis Trichardt; T., Wyllies Poort; T., Zoutpansberg distr., Limpopo R., along banks, nr Kobeehan, 660 m; T., Tsaneen, 600 m; SW. Waterberg distr.; T., Zululand, Hluhluwe, 600 m; T., 6 km W. of Klaserie; T., 23 km S. of Brugersfort, 990 m; T., 24.2 km W. of Pongola, 550 m; T., 17.7 km N. of Louis Trichardt, 800 m; T., 3.2 km NE. of Boyne, 1150 m; T., Klaserie, 600 m; T., Maritzberg; T., Limpopo R., 23°00'S, 27°57'E, 840 m; T., 11.3 km W. of Potgietersrus, 24°17'S, 28°57'E, c. 1170 m; Natal, Durban, Umbilo; N., Pipetown; N., Amanzimtoti; N., Tugela R. Canyon, 30.6 km N. of Kranskop, 450 m; N., St Lucia, 50 m. **Swaziland:** Border post.

**DISTRIBUTION** (Fig. 152, and Biogeography section, p. 156). Widely distributed in the eastern half of southern Africa.

**BIOLOGY.** Little is known of the biology of this species. Nolte (1939), in his comparative study of seven species of Acrididae in the Transvaal, states that adult females have 18 ovarioles per ovary.



Adults were mainly found from October to April but sometimes in July and August. The species has a chromosome complement of 11 autosomes and an XO sex determination system. *O. carvalhoi* has been reported damaging cotton in Mozambique (Del Valle y Marche, 1968).

DISCUSSION. The type-material of *O. carvalhoi* Bolivar from Lourenço Marques was originally deposited at Lisbon. Dr J. de A. Fernandez kindly informs me that it is lost. In order to guarantee stability of nomenclature a neotype male is here designated from the original type-locality.

*Oedaleus plenus* (Walker)  
(Figs 6, 22, 45, 96–99, 153)

*Epacromia plena* Walker, 1870: 769.

This species is divided into two subspecies under which the specific synonyms are separately listed below.

REDESCRIPTION. ♂. Integument finely rugulose. Antennae about one and a third times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, narrowing to about three-quarters of maximum width anteriorly; lateral carinae distinct; frons in profile slightly convex, frontal ridge constricted at vertex and below median ocellus, wider between antennal bases. Eyes one and two-fifths as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin from slightly acutangular to slightly obtusangular. Tegmen normal, surpassing hind knees by one-third to one-half of hind femur length. Hind tibia with 10 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and one-third times claw length; arolium three-fifths of claw length. Cerci little more than twice as long as basal width. Genitalia (Figs 96–98): cingular apodemes long, strongly curved; rami long; exposed portion of cingular valves and apical penis valves short, subapical ventral process rounded; anterior projections large, rounded; posterior projections rectangular.

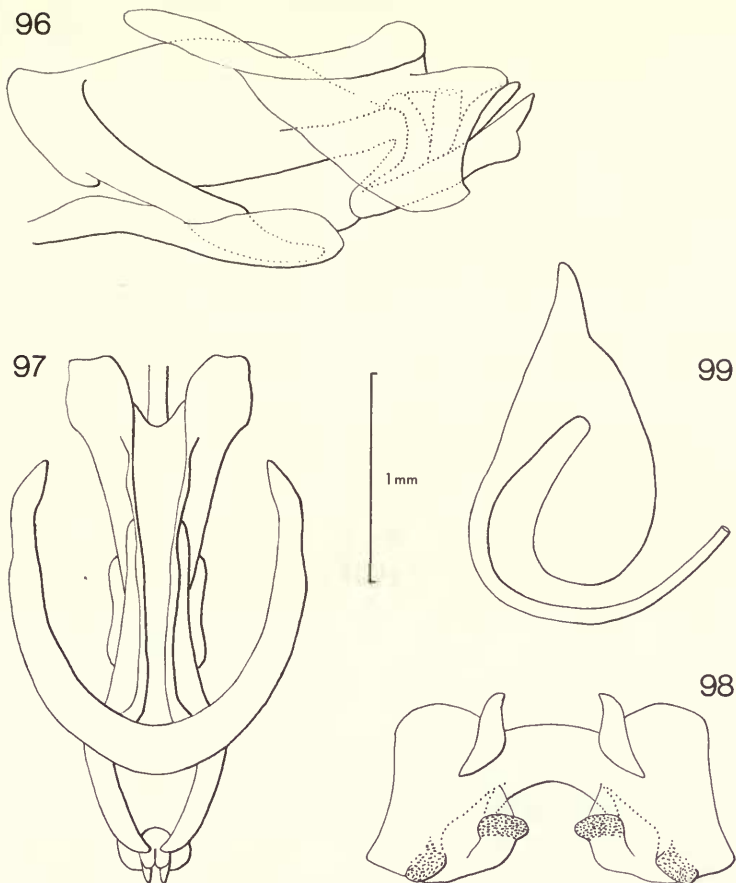
General coloration variable, brown, grey brown, or greenish; green forms rare, brown forms with lighter brown markings on frons, genae, and dorsal surface of pronotum, tegmen, and hind femur; green forms have green markings here and on vertex. Tegmen infuscate in basal half, with irregular pale transverse band one-third along from base usually extending from costal margin to subcostal vein but sometimes less developed; second band half way along usually reaches from costal margin to second cubitus but may be obscure or poorly developed; apical third of tegmen clear or speckled. Hind wing fascia (Fig. 6) incomplete, interrupted between first cubitus and first anal vein (in *O. plenus browni* more broadly interrupted or almost obsolete), reaching hind margin of wing posteriorly; basal area pale yellow or colourless, wing tip sometimes infumate. Hind femur with irregular transverse oblique bands on exterior surface and interior upper marginal area; interior medial area straw-coloured; ventral surface orange-red; hind tibia with dark basal ring, subbasal pale area, otherwise orange-red.

♀. Ventral ovipositor valves (Fig. 45) elongate, weakly sclerotized, longer than wide, exterior lateral margins only slightly excavated; basivalvular sclerite smooth. Spermatheca (Fig. 99) with conical, slightly recurved subapical diverticulum.

AFFINITIES. *O. plenus* is a member of the rather homogeneous group of species which includes *O. senegalensis* and *O. nigeriensis*, but is in some respects intermediate between this group and the *O. instillatus-obtusangulus-rosescens*-group, having a tendency to overall grey-brown coloration, with green forms rare, and epiphallic lophi with small, equal-sized lobes (Fig. 98).

DISTRIBUTION (Fig. 153, and Biogeography section, p. 156). Widely distributed in southern Africa, with a population in Tanzania, isolated on the northern edge of the *Brachystegia* woodland. The records from Namibia, Angola, and Zambia appear to be new. Johnsen & Forchhammer (1978) have recently recorded the species (as *O. dilutus*) from Botswana. The record by Dirsh (1956a: 325, 265) from Lesotho should be referred to *O. plenus browni* which is apparently restricted to high ground above about 1500 m in the eastern half of South Africa, and Lesotho.

BIOLOGY. Unknown. Cuthbertson (1934) reported this species among the prey of the asilid fly *Alcimus rubiginosus*.



**Figs 96–99** *O. plenus*, genitalia. 96, endophallus and cingulum, lateral view; 97, same, dorsal view; 98, epiphallus; 99, spermatheca.

The two subspecies of *O. plenus* may be separated by the following key.

- 1 Hind wing fascia absent or restricted to posterior half of wing, seldom passing third anal vein anteriorly but occasionally reaching posterior branch of second anal vein (*2Aa*) (E. Transvaal, E. Cape Province, Lesotho) . . . . . ***O. plenus browni*** subsp. n. (p. 121)
- Hind wing fascia only interrupted between first cubitus and first anal vein, reaching costal margin of wing anteriorly (southern Africa, NE. Tanzania) . . . . . ***O. plenus plenus*** (Walker) (p. 119)

***Oedaleus plenus plenus*** (Walker, 1870)

*Epacromia plena* Walker, 1870: 769. Lectotype ♂, SOUTH AFRICA (BMNH), designated by Uvarov (1925: 276) [examined].

*Oedaleus (Oedaleus) nigro-fasciatus* var. *caffer* Saussure, 1888: 41. LECTOTYPE ♀, SOUTH AFRICA (MHN, Geneva), here designated [examined]. [Synonymized by Uvarov, 1925: 276.]

*Oedalus* [sic] *plena* (Walker) Distant, 1892: 260.

*Chortoicetes plena* (Walker) Kirby, 1920b: 70.

*Oedaleus plenus* (Walker) Kirby, 1910: 225.

*Oedaleus caffer* Saussure; Kirby, 1910: 225.

*Oedaleus dilutus* Miller, 1929: 74. Holotype ♂, TANZANIA (BMNH) [examined]. **Syn. n.**

## MEASUREMENTS

Sample from SW. Africa: various localities.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26.18	3.6	4.73	19.59	12.32	3.33	3.70	4.15
Range	24.3–	3.3–	4.3–	18.3–	11.2–	3.1–	3.5–	3.8–
	27.4	3.8	5.1	20.7	12.85	3.6	3.9	4.6
S.D.	0.867	0.113	0.228	0.727	0.503	0.129	0.119	0.214
n	14	14	14	14	14	14	14	14

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	31.44	4.72	5.76	23.48	14.6	3.9	3.75	4.08
Range	29.0–	4.3–	5.3–	21.8–	13.3–	3.5–	3.4–	3.8–
	33.0	5.0	6.1	25.0	15.7	4.3	4.0	4.4
S.D.	1.202	0.188	0.239	0.887	0.676	0.234	0.194	0.177
n	15	15	15	15	15	15	15	15

## MATERIAL EXAMINED

*Epacromia plena* Walker, lectotype ♂, **South Africa**: no further data (*Smith?*) (BMNH). *Oedaleus nigrofasciatus* var. *caffer* Saussure, lectotype ♀, **South Africa**: no further data (*Delalande*) (MHN, Geneva). *Oedaleus dilutus* Miller, holotype ♂, **Tanzania**: Dodoma, Kitope, 6.iv.1927 (*Miller*) (BMNH).

In addition to the types, 276 specimens were examined from the following localities. **South Africa**: 3 ♂, 2 ♀, no further data (*Smith?*) (including 2 ♂, 2 ♀, paralectotypes of *Epacromia plena* Walker); 1 ♂, 'Cape', no further data (paralectotype of *E. plena* Walker); Transvaal, Rustenburg; T., Wyllies Poort; T., Pretoria; T., Tom Burke, 23°04'S, 28°00'E; T., Johannesburg; T., Klaserie, nature area, Klaserie R.; T., 24.2 km W. of Pongola, 550 m; T., 33.8 km S. of Messina, 660 m; T., 3.2 km S. of Messina, 590 m; T., 17.7 km N. of Louis Trichardt, 800 m; T., Skukuza; T., Zebediela; T., Messina; T., Metsimaklaba; Cape Province, Ceres; C.P., Nieuwoudtville; C.P., Queenstown, 1050 m; C.P., 8 km NW. of Craddock; C.P., Grahamstown; C.P., 35.4 km W. of Cofimvaba, 940 m; C.P., Cape of Good Hope; C.P., Namaqualand; C.P., Spektakel Pass, 29 km W. of Springbok; C.P., Skeerpoort. **Namibia**: Gobiswater farm, 19.3 km N. of Grootfontein; Kombat; 17°59'S, 16°02'E, 1110 m; Swakop R., 4.8 km S. of Okahandja; Rietfontein, 37 km SW. of Grootfontein; Otavie; Okahandja; Damaraland, c. 8 km W. of Grootfontein, 1470 m; Otjitambi farm, 43.5 km ESE. of Kamanjab; Otjikoko Süd farm, 53 km ENE. of Omaruru; Regenstein, 24 km SSW. of Windhoek; Onguma farm, 88.6 km NW. of Tsumeb; Ameib farm; 30.6 km NW. of Karibib; 25.8 km E. of Gobabis; 3.2 km NW. of Ontjo, 1250 m; 9.7 km W. of Windhoek, 8.v.1958, 1660 m; 60 km W. of Windhoek, 14.iii.1972; 13 km N. of Rehoboth; 50 km W. of Omaruru; Okahandja bis, Waterberg; Namib. **Botswana**: Maun; Gaborones; Nokaning; Selinda spillway; Kwebe Hills; Kasana; Ngamiland, 20°S, 23°E; Ghanzi, Mongalatsiba; Kalahari; 59.6 km S. of Francistown, 21°37'S, 27°21'E; L. Ngami, 19.3 km NE. of Sehithwa; 29 km NE. of Kalkfontein; 16 km NE. of Ghanzi; Moremi reserve, 19°23'S, 23°33'E; 40.3 km W. of Gweta, 20°17'S, 25°54'E; Kuke pan, 20°59'S, 22°25'E; 67.6 km W. of Kalkfontein; 4.8 km NE. of Maun; nr Moremi res., 19°27'S, 23°45'E; Kaotwe. **Angola**: Tundavala, 13–16 km NW. of Sa da Bandeira; Rocadas, mopane scrub; Otchifengo R., Iona Nat. Pk; Huila distr., Cahama. **Zimbabwe**: Odzi distr., Matopo Hills; Shamva, 930 m; Victoria Falls, 900 m; Shangani, de Beers ranch; Selukwe, 1120 m; Balla Balla; 22.5 km NW. of Beitbridge, 540 m; 87 km S. of Umtali, 560 m; West Nicholson, Masase. **Zambia**: Livingstone. **Tanzania**: 1 ♀, Tindiga, 20.xi.1926 (*Miller*) (paratype of *O. dilutus* Miller); S. of Usasi, clearings, 72.5 km NW. of Singida; Kondoia to Irangi; Ruaha Nat. Pk.

**DISCUSSION.** Walker's type-material almost certainly came from south-west Cape Province. Specimens from this climatically distinct zone usually have the posterior arms of the pronotal X-marking thin, less than one and a half times as wide as the anterior arms, whereas elsewhere the posterior arms are usually about three times as wide as the anterior arms. Despite the evident discontinuity in the distribution of this character (Fig. 153) it is not an absolutely reliable distinction between populations, so the name *O. plenus plenus* is here used to refer to all the material available whatever its pronotal characteristics, except for material referred to *O. plenus browni* for other reasons.



Miller's *O. dilutus*, described from Tanzania, is identical in all respects with material from south of the *Brachystegia* woodland zone and is here considered to be a junior synonym of *O. plenus plenus*. If the SW. Cape population should later be conclusively shown to have consistent characters meriting subspecies status then the name *O. plenus plenus* could be restricted to this population and *dilutus* would again be available for material of the species from other areas. Measurements of eight males and seven females from SW. Cape Province, including Walker's type-series, were found to give rather high mean values for the length/depth ratio of the hind femur (FL/FD: 4.00 ♂, 4.09 ♀). There is, however, a likelihood of bias with such low numbers and dubious locality data and a study of fresh material from this area is needed.

*O. nigrofasciatus* var. *caffers* Saussure, 1888, synonymized with *O. plenus* by Uvarov (1925), was originally described from 'Africa meridionalis'. There are several specimens of *O. plenus* in the MHN, Geneva, of which only one female is labelled in Saussure's own hand 'var. afr. merid.'. This specimen is accordingly here designated as the lectotype of *O. nigrofasciatus* var. *caffers*. The status of the remaining material (3 ♂, 7 ♀) in the MHN Geneva is not clear and paralectotypes have therefore not been designated.

*Oedaleus plenus browni* subsp. n.

MEASUREMENTS (type-series)

		Males						
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23.16	3.74	4.57	16.85	12.26	3.51	3.49	3.73
Range	22.2–	3.3–	4.2–	15.8–	11.1–	3.3–	3.3–	3.5–
	24.1	4.1	5.1	18.1	13.6	3.9	3.6	4.0
S.D.	0.658	0.247	0.287	0.769	0.742	0.188	0.111	0.168
n	6	9	9	7	9	9	9	7

		Females						
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	30.28	5.22	5.81	21.92	15.13	4.27	3.55	3.78
Range	29.1–	4.8–	5.1–	20.3–	14.0–	3.9–	3.4–	3.5–
	31.6	5.6	6.3	24.0	15.9	4.6	3.7	4.0
S.D.	1.012	0.275	0.461	1.489	0.703	0.246	0.116	0.164
n	5	6	6	6	5	5	5	6

MATERIAL EXAMINED.

Holotype ♂, **South Africa:** Cape Province, De Aar, 13.ii.1959 (*Brown*) (DATS, Pretoria).

Paratypes, **South Africa:** 3 ♂, 1 ♀, Orange Free State, Bosrand, Afdeling farm, 30.iii.1934 (*Ogilvie*); 1 ♂, O.F.S., Mafeking, 28.ii.1934 (*Ogilvie*); 1 ♂, O.F.S., Bloemfontein, 13.ii.1918; 1 ♀, same data, 10.iv.1918; 1 ♂, same data, 13.iv.1951 (*Botha*); 1 ♀, O.F.S., Petrus, 23.i.1919; 1 ♂, O.F.S., Bloemfontein, xii.1931 (*Key*) (ANIC, Canberra); 1 ♀, Transvaal, Pretoria (*Distant*); 1 ♀, Cape Province, De Aar, 13.ii.1959 (*Brown*) (DATS, Pretoria); 2 ♂, C.P., 22.5 km E. of Middleburg, 8–14.xii.1960 (*Brown, Fürst & Haacke*) (DATS, Pretoria). **Lesotho:** 1 ♀, Maseru, Lancer's Gap, 22.iii.1951 (*Brinck & Rudebeck*).

DISCUSSION. In addition to the characters mentioned in the key, interesting differences between the morphometrics of *O. plenus browni* and the nominate subspecies are revealed when mean measurements are compared by 't' test. Femur length and pronotum length do not differ significantly, but in females head width is very significantly greater in *O. p. browni* than in *O. p. plenus* ( $P < 0.001$ ), while tegmen length is significantly less, particularly in the male ( $P < 0.001$  ♂,  $< 0.05$  ♀). Head width variation is enigmatic, but decrease in wing length is very commonly associated with adaptation to montane conditions in grasshoppers at and below species level. Not surprisingly TL/PL is significantly greater in the nominate subspecies ( $P < 0.001$  ♂,  $< 0.002$  ♀) than in *O. p. browni* but less accountably the FL/FD ratio is also higher in the former than the latter

( $P < 0.001$  ♂,  $< 0.002$  ♀). Presumably decreasing flight capability is correlated with decreased take-off capability in the form of shorter femora.

The new subspecies is named in honour of its discoverer, Dr H. D. Brown.

***Oedaleus decorus*** (Germar, 1826)  
(Figs 11, 28, 29, 51, 100–106, 158, 163)

*Acrydium decorum* Germar, 1826: pl. 17.

This species is here divided into two subspecies under which the specific synonyms are separately listed below.

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae about one and a third times as long as head and pronotum together, flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to two-fifths of maximum width anteriorly; lateral carinae distinct, faint median carina sometimes visible; frons in profile straight or slightly convex; frontal ridge, slightly expanded and coarsely punctate between antennal bases. Eyes about one and two-fifths as long as wide. Pronotum low tectiform; median carina arcuate, not intersected by posterior sulcus. Tegmen surpassing hind knees by about one-third of femur length. Hind tibia with 11–12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment about twice claw length; arolium half claw length. Cerci about twice as long as basal width. Genitalia (Figs 100–105): cingular apodemes normal, rami well developed, cingular and apical penis valves short; subapical ventral process small; epiphallus variable, trapezoidal, with thick bridge; inner and outer lobes of lophi of equal size; anterior projections large, rounded; posterior projections rectangular.

General coloration variable, brown, with light brown or green markings on frons, genae, pronotum, basal quarter of tegmina, and hind femora. Tegmen infusate brown in basal half with variable transverse pale bands situated one-sixth, one-third, and one-half along from base; apical half clear with brown specks. Hind wing fascia (Fig. 11) complete, not reaching hind margin of wing, wing tip tinged with brown; basal area of wing pale yellow with distinct pale bluish tinge on wing vein bases. Hind femora with three oblique transverse bands on inner and outer surfaces, ventral surface red, knees black; hind tibiae with black basal ring, basal one-third pale straw-coloured, apical two-thirds reddish.

♀. Frons in profile convex. Ventral ovipositor valves (Fig. 51) blunt, strongly sclerotized. Spermatheca (Fig. 106) with apical diverticulum bulbous with acutely rounded apex, and short subapical diverticulum.

AFFINITIES. *O. decorus* is most closely allied to *O. senegalensis*, *O. nigeriensis* and *O. infernalis* in having strongly transverse inner lobes to the epiphallic lophi. The red ventral surface of the hind femur is shared with *O. infernalis* from which, however, *O. decorus* is easily distinguished by its general coloration, and the form of the pronotal X-marking and hind wing fascia.

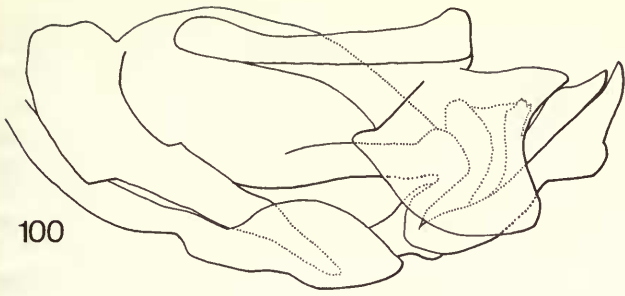
DISTRIBUTION (Figs 158, 163, and Biogeography section, pp. 161, 165). Europe, North Africa, Middle East, with subspecies *decorus* extending into SW. Russia, and subspecies *asiaticus* continuing eastwards across Transbaikalia, Mongolia and China.

BIOLOGY. *O. decorus* has probably received more attention than any other species in the genus except *O. senegalensis*. Adults of *O. decorus decorus* are found in North Africa from June until January and in the Middle East from April to September. In southern Europe they occur from May to October with a gradually shortening and later season towards the northern limit of the species. *O. decorus asiaticus* has been recorded in eastern U.S.S.R., Mongolia, and China from July to September. It is probable that one generation is the norm outside Africa. However, the longer season in North Africa may allow a second generation, since laying has been reported in July (A-L.R.C. Unpublished Report 6114-135) in Libya. Berezkhov (1956) gives five as the number of nymphal instars. The egg pod has been described by Zimin (1938), and Morales Agacino (1951), who found 10 to 35 eggs per pod. Waloff (1954) records 18 and 20 ovarioles per ovary in two females dissected.

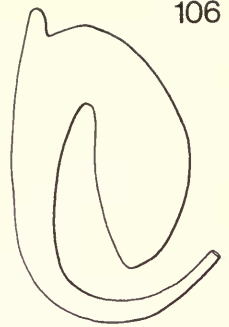
Ivanov (1934) made a study of the biology and ecology of *O. decorus* in Central Asia and Stebaev (1957) found that it was seasonally mobile between different types of habitat. It was recorded in the

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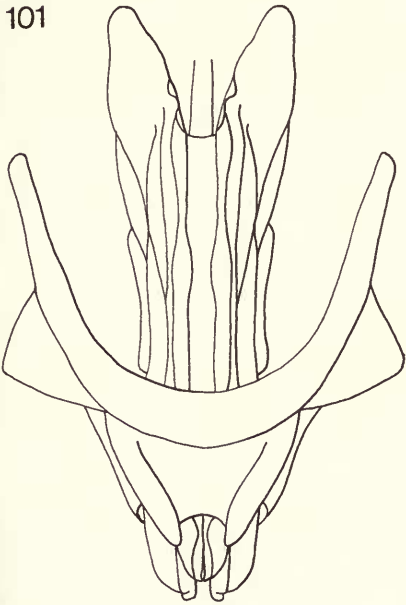
**Figs 100–106** *O. decorus*, genitalia. 100–102, *O. decorus decorus*; (100) endophallus and cingulum, lateral view; (101) same, dorsal view; (102) epiphallus. 103–105, *O. decorus asiaticus*; (103) endophallus and cingulum, lateral view; (104) same, dorsal view; (105) epiphallus. 106, *O. decorus decorus*, spermatheca.



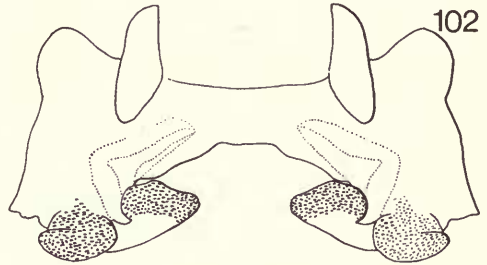
100



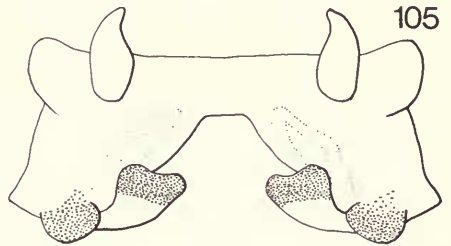
106



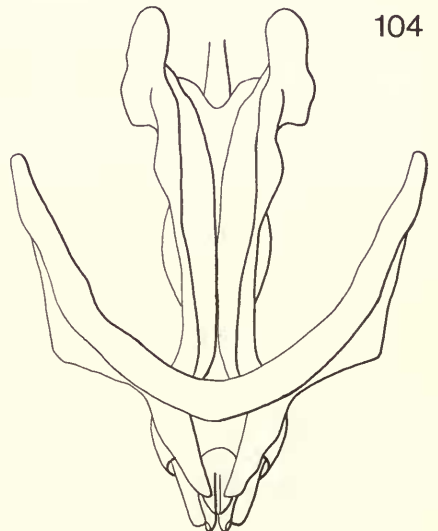
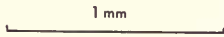
101



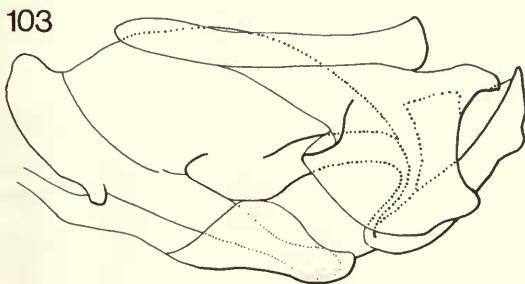
102



105



104



103



French Alps up to 1300 m by Dreux (1961) who stated that the species distribution in France is bounded by the 16° July isotherm. In U.S.S.R. Bei-Bienko & Mishchenko (1951a) regarded it as a characteristic species of stony mountain sides with xerophytic vegetation, and in the Pyrenees Marty (1969) found that this species constituted 20% of all Orthoptera in the littoral zone. In Turkestan (Zacher, 1949) the species lays in damp areas with *Cynodon dactylon* and *Hordeum murinum*. *O. decorus* has been reported damaging wheat, vines and lentils in Libya (A-L.R.C. Unpublished Report 6114-135), maize and tobacco in Morocco (Lépiney & Mimeur, 1932) and cotton, lucerne and wheat in Iran (Farahbaksh, 1961). *O. decorus asiaticus* was described as a pasture pest in Transbaikalia region (Bei-Bienko & Mishchenko, 1951b). Predation of adults of *O. decorus* by asilid flies was reported by Adamovic (1968) and four species of *Blaesoxipha* (Greathead, 1963; Léonide & Léonide, 1969; 1973) and one Nemestrinid (Léonide, 1963) have been reared from adults. Integumental coloration in relation to humidity, temperature, and background colour have been studied by Jovančić (1953) and Ergene (1954; 1955a; 1955b; 1955c; 1956). The thoracic repugnatorial gland has been described by Vosseler (1902c), and Hollande (1926) who mistakenly considered the gland to be eversible.

The two subspecies of *O. decorus* may be separated by the following key.

- 1 Generally larger (except in northern France), body length 24.0–36.3 mm male, 31.1–49.0 mm female; pronotal hind margin more angular (Fig. 28); hind wing fascia thicker, and terminating posteriorly within 1 mm of wing margin (Fig. 11); interior surface of epiphallic bridge weakly arched (Fig. 102) (North Africa, S. Europe, Middle East, SW. U.S.S.R. as far as E. Kazakh S.S.R., W. Sinkiang province of China). . . . . *O. decorus decorus* (Germar) (p. 124)
- Generally smaller, body length 25.0–27.5 mm male, 32.0–37.6 mm female; pronotal hind margin more rounded (Fig. 29); hind wing fascia thinner, terminating posteriorly more than 1 mm from wing margin; interior surface of epiphallic bridge strongly arched (Fig. 105) (Mongolia, Transbaikalia, Hopeh and Shantung provinces of China). . . . . *O. decorus asiaticus* Bei-Bienko (p. 126)

### *Oedaleus decorus decorus* (Germar, 1826)

*Acridium decorum* Germar, 1826: pl. 17. Holotype ♂ (?), U.S.S.R.: 'Podolia australi (Besser)' (Mus. Besseri) (lost). NEOTYPE ♂, U.S.S.R.: Daghestan (BMNH), here designated [examined].

[*Acridium flavum* (Linnaeus); Costa, 1836: 11. Misidentification.]

[*Oedaleus nigrofasciatus* (Degeer); Bormans, 1879: 407; Brunner, 1882: 169; Bonnet & Finot, 1884: 220; Bormans, 1884: 179; 1885: 109; Olivier, 1892: 45; Frey-Gessner, 1894: 106; Finot, 1895: 479; Krauss & Vosseler, 1896: 531; Fenard, 1896: 107; Bolivar, 1898: 76; Burr, 1898: 179; Vosseler, 1902a: 359; 1902b: 116; 1902c: 84; Finot, 1902: 434; Giglio-Tos, 1907: 8; Burr, 1912: 31; Bolivar, 1914: 188; Werner, 1914: 397; Steck, 1915: xiv; Plotnikov, 1921: 9; Giglio-Tos, 1923: 5; Rabaud, 1923: 18; Zanon, 1924: 246; Salfi, 1925: 93; Hollande, 1926: 374; Werner, 1934: 6; Jovančić, 1953: 99; Barbut, 1954: 339; Costantino, 1954: 4. Misidentifications.]

[*Oedipoda nigrofasciata* (Degeer); Serville, 1831: 288; Burmeister, 1838: 645. Misidentifications.]

[*Acrydium nigrofasciatum* (Degeer); Latreille, 1805: 157. Misidentification.]

[*Gryllus nigrofasciatus* (Degeer); Charpentier, 1825: 140. Misidentification.]

[*Gryllus flavus* (Linnaeus); Rambur, 1838: 82. Misidentification; Uvarov, 1948: 384.]

*Oedaleus decorus* (Germar) Uvarov, 1923: 69.

#### MEASUREMENTS

Sample from Algeria: Djelfa, 9.x.38 (*M. N. Korsakoff*).

#### Mailes

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38.2	5.69	6.23	28.27	18.86	4.42	4.27	4.56
Range	32.8–43.2	5.1–6.2	5.2–7.4	23.6–31.3	16.3–21.7	3.8–5.1	4.0–4.6	4.1–5.0
S.D.	2.55	0.27	0.525	1.890	1.39	0.32	0.17	0.17
n	27	27	27	23	26	26	26	23



Sample from Western U.S.S.R.: various localities.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27.92	4.31	4.44	20.6	14.26	3.39	4.23	4.66
Range	26.1–30.4	3.9–4.7	3.9–5.1	18.9–22.5	12.9–15.7	3.0–4.0	3.5–4.5	4.2–5.2
S.D.	1.35	0.28	0.37	1.16	0.92	0.32	0.32	0.35
n	8	8	8	8	7	7	7	8

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38.87	6.22	6.27	28.8	19.16	4.57	4.2	4.61
Range	33.0–42.1	5.1–6.9	4.9–7.1	24.8–30.9	15.7–20.7	3.65–5.0	4.0–4.3	4.3–5.1
S.D.	2.64	0.47	0.61	1.9	1.62	0.45	0.13	0.29
n	9	9	9	9	7	7	7	7

## MATERIAL EXAMINED

*Acrydium decorum* Germar, neotype ♂, U.S.S.R.: Dagestan, Chodz-Tau, 5.vii.1924 (*Riabov*) (BMNH).

In addition to the neotype, a total of 750 specimens of this subspecies were examined from the following countries: Morocco, Algeria, Tunisia, Libya, Lebanon, Syria, Israel, Iraq, Turkey, Iran, Afghanistan, U.S.S.R., Rumania, Bulgaria, Greece, Albania, Yugoslavia, Czechoslovakia, Switzerland, Italy, Sicily, Corsica, France, Spain, Portugal, Madeira, Canary Is.

**DISCUSSION.** The measurements and 't' tests indicate the very considerable range of variation in morphometrics shown by this subspecies. The largest specimens, judged by femur or tegmen length, are found in Algeria, but from here northwards through western Europe there is a decline in size, with specimens from Gironde on the west coast of France significantly smaller than those from the Rhône delta in all respects, and with a significantly higher ratio of tegmen length to pronotum length and a significantly thicker femur in relation to its length. Surprisingly, the Rhône delta specimens are closest to those from the western U.S.S.R. in all measurements though differing significantly from them in the female femur length.

The type-material of *Acrydium decorum* has not been mentioned in the taxonomic literature since Germar's original description (1826) apart from repetition of the details given by him. The material was in the collection of V. S. Besser which later passed to the Zoological Museum of Kiev State University. I am indebted to Dr L. Pisareva for the information that the type cannot be found there. Since the type-material of this species is no longer extant a neotype is here designated from the south-west U.S.S.R.

*Oedaleus decorus asiaticus* Bei-Bienko, 1941 stat. n.

*Oedaleus asiaticus* Bei-Bienko, 1941: 152. Holotype ♂, U.S.S.R.: Buryat A.S.S.R., Kiakhta distr., Ust' Kiakhta, 20.viii.29 (*A. N. Strakhovskiy*), (ZI, Leningrad).

## MEASUREMENTS (all available material)

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25.73	3.65	3.84	19.11	12.09	2.85	4.24	4.98
Range	24.9–27.5	3.5–3.8	3.6–4.2	18.2–21.0	11.7–12.5	2.8–2.9	4.1–4.4	4.7–5.3
S.D.	0.926	0.071	0.22	0.95	0.25	0.034	0.12	0.19
n	6	6	6	6	5	5	5	6



Females

Mean	35.79	4.41	5.57	26.33	16.29	3.75	4.34	4.74
Range	32.1–	4.9–	4.9–	23.9–	14.9–	3.4–	4.2–	4.5–
	37.7	5.8	5.8	28.4	18.2	4.1	4.5	5.1
S.D.	1.80	0.26	0.37	1.24	0.92	0.19	0.082	0.175
n	9	9	9	9	9	9	9	9

Significance levels of 't' tests on comparisons of mean measurements of populations of *O. decorus*

Paired comparisons of mean values	Sex	Head width	Pronotum length	Tegmen length	Femur length	FL/FD	TL/PL
Algeria/Bouches du Rhône	♂	< 0.001	< 0.001	< 0.001	< 0.001	n.s.	n.s.
	♀	< 0.001	< 0.02	< 0.02	n.s.	n.s.	n.s.
BDR/Gironde	♂	< 0.001	< 0.01	< 0.001	< 0.001	< 0.02	< 0.001
	♀	< 0.001	< 0.001	< 0.001	< 0.001	< 0.01	< 0.01
BDR/Russia	♂	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	♀	n.s.	n.s.	n.s.	< 0.05	n.s.	n.s.
Gironde/Russia	♂	< 0.001	n.s.	< 0.001	< 0.002	n.s.	n.s.
	♀	< 0.001	n.s.	< 0.001	< 0.002	< 0.01	< 0.05
Gironde/ <i>asiaticus</i>	♂	< 0.05	< 0.01	n.s.	< 0.05	< 0.05	n.s.
	♀	n.s.	n.s.	< 0.05	n.s.	< 0.001	n.s.
Russia/ <i>asiaticus</i>	♂	< 0.001	< 0.01	< 0.05	< 0.001	n.s.	< 0.05
	♀	< 0.001	< 0.01	< 0.01	< 0.001	< 0.05	n.s.

MATERIAL EXAMINED

**U.S.S.R.:** 1 ♀, Transbaikal reg., mouth of R. Kīran, 10.ix.1929 (*Mikhno*) ZI, Leningrad (paratype of *Oedaleus asiaticus* Bei-Bienko); 1 ♂, 1 ♀, Transbaikal reg., Ust' Kyakhta dist., 20.vii.1929 (*Strakhovskiy*) (ZI, Leningrad) (paratypes of *O. asiaticus* Bei-Bienko); 1 ♀, Transbaikal reg., Troitskosavsk dist., 28.viii.1929 (*Mikhno*); 1 ♂, Minusinsk steppe, 29.vii.1924 (*Filipyev*); 1 ♂, Minusinsk, 30.vii.1924 (*Filipyev*) (ANS, Philadelphia); 1 ♀, same data, 21.viii.1924 (ANS, Philadelphia); 2 ♀, Transbaikal reg., Ust' Kyakhta dist., 20.viii.1929 (*Strakhovskiy*) (ANS, Philadelphia); 1 ♀, Troitskosavsk dist., Kapcheranka, 4.ix.1929 (*Mikhno*) (ANS, Philadelphia); 1 ♂, Minusinsk, Tagarsk I., 21.viii.1924 (*Filipyev*). **Mongolia:** 1 ♂, 1 ♀, Altai reg., W. foothills of Ikhe Bogdo, 21.viii.1926 (*Kiprichenko*) (ZI, Leningrad) (paratypes of *O. asiaticus* Bei-Bienko). **China:** 1 ♂, Peiping, 2.viii.1934 (*Chang?*) (USNM, Washington); 1 ♀, Shantung pr., O-ku, 18.viii.1934 (*Chang?*) (USNM, Washington).

**DISCUSSION.** Material of *O. decorus asiaticus* from eastern U.S.S.R. and China differs significantly in all measurements from material of the nominate subspecies in the western U.S.S.R., although in the two ratios differences are less marked. This might suggest morphometric support for the separate species status of *asiaticus*, but overall there is an equally significant difference between the western U.S.S.R. material and that from the Gironde region of western France. Comparing material of *asiaticus* with Gironde specimens, differences are generally of low significance (< 5 > %) or none at all excepting pronotum length, which in male *asiaticus* is markedly smaller, and the femur length to depth ratio (FL/FD), which is significantly smaller in the Gironde population than in *asiaticus*.

Bei-Bienko & Mishchenko (1951b: 578, 579) distinguish *asiaticus* from *decorus* on the basis of minor differences of coloration and shape which have not been found reliable in the material used in this study. At present *asiaticus* is considered as a subspecies or race of *decorus* but may prove on further study not to justify even racial status. Its small size and rounded posterior angle of the pronotum are features also found in specimens from Gironde and elsewhere on the north-western limit of the species distribution in France, and are probably a response to harsh conditions in both cases.

*Oedaleus infernalis* Saussure, 1884  
(Figs 5, 36, 52, 107–110, 163)

*Oedaleus (Oedaleus) infernalis* Saussure, 1884: 116. LECTOTYPE ♂, JAPAN (NM, Vienna), here designated [examined].

*Oedaleus (Oedaleus) infernalis* var? Saussure, 1884: 117. [Based on 1 ♂, U.S.S.R.: Amur (NM, Vienna), see below.]

*Oedaleus infernalis* var. *amurensis* Ikonnikov, 1911: 255. LECTOTYPE ♂, U.S.S.R.: Amur (NM, Vienna), here designated [examined]. [Varietal name erroneously attributed to Saussure, op. cit.] **Syn. n.**

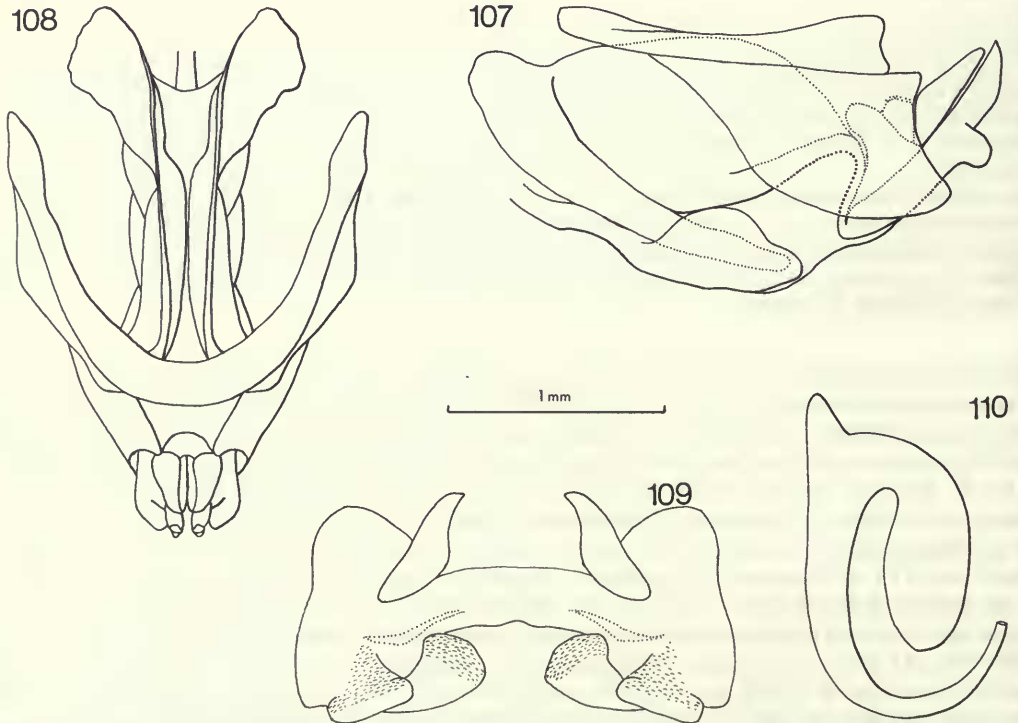
*Oedaleus infernalis amurensis* Ikonnikov; Bei-Bienko, 1941: 154.

*Oedaleus manjius* Chang, 1939: 21. Holotype ♂, CHINA: Chekiang, Wenchow, 15.ix.1933 (*K. S. Chang*) (lost). **Syn. n.**

*Oedaleus infernalis montanus* Bei-Bienko in Bei-Bienko & Mishchenko, 1951b: 577. Holotype ♂, CHINA: N. slope of Burkhan-Budda, defile Khatu, c. 10,800 ft [3300 m], end vi- beginning vii. 1901 (*P. C. Kozlov*) (ZI, Leningrad). **Syn. n.**

*Oedaleus infernalis* Saussure; Jacobson & Bianchi, 1905: 256.

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae barely longer than head and pronotum together; flagellum 24-segmented. Fastigium of vertex as long as wide, concave with raised margins, narrowing to half maximum width anteriorly. Frons in profile convex, frontal ridge constricted at vertex and below median ocellus, ventrally obsolescent. Eyes about one and a third times as deep as wide. Pronotum tectiform, median carina arcuate, lateral lobes coarsely punctate in metazona, hind margin acutangular to rectangular. Tegmen surpassing folded hind knees by one-quarter to one-half of hind femur length. Hind tibia with 12 inner and 12 outer spines; inner apical spurs less than twice length of outer; apical tarsal segment more than two and a half times claw length; arolium little more than half claw length. Cerci about twice as long as wide. Genitalia (Figs 107–109): rami, apodemes, cingular and apical penis valves of moderate length; subapical process large and protruding; epiphallus rectangular, twice as long as wide; outer lobes of lophi wider than inner lobes; anterior projections large, rounded; posterior projections small.



Figs 107–110 *O. infernalis*, genitalia. 107, endophallus and cingulum, lateral view; 108, same, dorsal view; 109, epiphallus; 110, spermatheca.

General coloration dark mottled brown, occasionally green. Brown form with pale X-marking on pronotum (♀, Fig. 36), and pale band on genae; green form with variable degree of green on frons, genae, pronotum (obscuring X-marking), thorax and hind femora. Tegmen infusate in basal half with four variable pale transverse bands extending from costal margin. First band one-sixth along from base, reaching subcostal vein, sometimes obsolete; second band one-third along, reaching first or second cubitus; third band half along, reaching *Cu1c* or *Cu2*; fourth band two-thirds along, variable, often reaching hind margin but without a distinct border towards apex of wing which is clear with variable dark patches. Hind wing fascia (Fig. 5) complete; wing tip infumate, basal area pale yellow. Hind femur with 3 variable oblique transverse dark bands on external and internal surface. On internal surface two basal bands combine to form U-shaped marking in medial area. Ventral surface of hind femur red, sometimes faded; hind knees black; tibiae basally black, subbasally pale straw (sometimes tinged with red), remainder red.

♀. Hind tibiae and ventral surface of hind femur brown, not red. Ventral ovipositor valves (Fig. 52) elongated and ridged; basivalvular sclerite rugose. Spermatheca (Fig. 110) with short conical subapical diverticulum.

## MEASUREMENTS

Sample from Japan: Nishigo, Uzen.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	31.45	4.43	5.73	23.37	16.52	4.18	3.95	4.08
Range	28.7–34.8	4.2–4.7	5.3–6.2	21.2–26.3	15.2–17.8	3.9–4.5	3.8–4.2	3.8–4.4
S.D.	1.377	0.144	0.259	1.229	0.697	0.155	0.109	0.142
n	21	21	21	21	21	21	21	21

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	42.29	6.28	7.88	31.28	22.03	5.37	4.10	3.97
Range	38.6–45.8	6.0–6.9	7.4–8.7	28.0–34.1	20.7–25.5	5.0–6.0	3.9–4.3	3.7–4.2
S.D.	1.912	0.246	0.378	1.616	1.146	0.242	0.113	0.157
n	19	19	19	19	19	19	19	19

Sample of '*amurensis*', from E. Manchuria and Ussuri region of U.S.S.R. around L. Khanka, including lectotype.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25.9	3.71	4.66	19.01	12.98	3.30	3.96	4.08
Range	23.7–30.6	3.5–4.1	4.2–5.1	17.1–23.2	11.9–14.3	3.0–3.65	3.5–4.3	3.4–4.4
S.D.	1.957	0.163	0.350	1.608	0.870	0.178	0.185	0.158
n	12	13	13	13	13	12	12	13

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	38.71	5.66	7.05	28.65	18.58	4.71	3.95	4.06
Range	34.5–46.8	5.2–6.4	6.3–8.2	25.3–35.7	17.2–19.1	4.3–5.3	3.6–4.2	3.8–4.4
S.D.	3.806	0.394	0.654	3.295	1.180	0.319	0.163	0.201
n	10	10	10	10	9	9	9	10



Sample of '*montanus*' ♂ paratype and 2 ♀ from China: Lifan, Szechuan.

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂	22.6	3.6	4.2	15.9	12.2	3.4	3.7	3.7
♀	38.3	6.2	8.0	28.1	20.6	5.6	3.7	3.5
♀	53.9	7.6	10.2	40.2	23.2	6.0	3.9	4.0

Sample of '*manjius*' from China: Szechuan, Wei Chow, 65 mls NW. of Chengtu, 5000 ft [1500 m]; viii.33 (*D. C. Graham*).

#### Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26.01	4.04	5.02	18.65	13.98	3.77	3.70	3.71
Range	23.3–29.2	3.7–4.4	4.5–5.8	16.5–21.9	13.3–14.8	3.6–4.0	3.6–3.8	3.4–3.9
S.D.	2.039	0.198	0.352	1.766	0.449	0.096	0.077	0.149
n	12	12	12	12	8	8	8	12

#### Females

Mean	36.01	5.96	7.33	25.83	18.75	5.0	3.76	3.53
Range	32.1–40.3	5.4–6.8	6.4–8.4	23.3–29.3	17.0–20.4	4.5–5.8	3.5–4.2	3.3–3.8
S.D.	2.097	0.320	0.509	1.491	1.011	0.294	0.140	0.135
n	25	25	25	25	25	25	25	25

**AFFINITIES.** *O. infernalis* is most closely related to *O. decorus* by its overall shape, the continuous band of the hind wing and the red ventral surface of the hind femur. It is, however, easily distinguished by its more sombre pattern, the poorly defined pronotal X-marking (Fig. 36) and hind wing fascia (Fig. 5), and the rather short cingular rami of the male genitalia (Fig. 108). The bases of the main veins of the hind wing are never tinged with pale blue in this species. In the female the ventral ovipositor valves are longer and more ridged than those of *O. decorus* (Figs 52, 51).

#### MATERIAL EXAMINED

*Oedaleus infernalis* Saussure, lectotype ♂, **Japan**: no further data (NM, Vienna). *Oedaleus infernalis* var. *amurensis* Ikonnikov, lectotype ♂, **U.S.S.R.**: Amur (NM, Vienna).

In addition to the types, 447 specimens were examined from the following localities. **Japan**: Tokyo; Takayama, Myjagi; Nagasaki; Yamashiro I., Kyoto; Yokohama; Nishigo, Uzen; Yamanaka Lake, Honshiu; 2 ♀, 'Japan', no further data (NM, Vienna) (paralectotypes of *Oedaleus infernalis* Saussure). **U.S.S.R.**: Kamen-Rybolov, L. Khanka, S. mouth; Ussuri Region, Spassk distr., Yakovlevka, woodland in inundation zone of R. Daubikhe; E. Siberia, Ussuri Reg., Spassk distr., Schmakovka; Ussuri Reg., R. Lyan-chi-khe; Siberia, 44°30'N, 133°00'E; E. Siberia, Kamen-Rybolov. **China**: Shense Pr., Taipaishan; N. Chihli Pr., Chih Feng; Chee Foo; Manchuria, Kuangning; Manchuria, L. Khanka; Nanking; Tientsin; Peking; 14 ♂, 50 ♀, 5 nymphs, Szechuan, Wei-Chow, 105 km N. of Chengtu, 1500 m, viii.33 (*Graham*) (USNM, Washington) (1 ♀ labelled '*Oedaleus wenchowensis* Chang det. Chang 1936'); Szechuan, Wenchuan; Szechuan, Wen Chuan Shien, 48 km NNW. of Kuan Shien, 1500–2250 m; Szechuan, Wei Chow, 105 km NW. of Chengtu, 1650–2700 m; Szechuan, between Li Fan and Wen Chuan Shien, 48.3 km NNW. of Kuan Shien, 1650–1950 m; Szechuan, O-Er, 42 km N. of Li Fan, 2700 m; Szechuan, Suifu; Peiping, Yenching University; Chekiang, Unchia; Chekiang, Ching'tien; Shantung; Mt Foochow; Mice River flats, Fu-chou, Fukien; Szechuan, Mt Omei, Baian-kara-ula range; Szechuan, Kwanhsien, 900m; Szechuan, nr Wenchuan, 1500–2100 m; Tseo Jia Geo, S. of Suifu, 420–600 m; Kong Shien, S. of Suifu, 420 m; 1 ♂, Szechuan, Li Fan, 10.viii.1893 (*Potan*) (ZI, Leningrad) (paratype of *Oedaleus infernalis montanus* Bei-Bienko); Ming tomb; Manchuria, Chin San; Foochow; Shantung peninsula, Yen-t'ai (Chefoo); Kiautschougebiet, Tsingtau; E.

China, Chen-Kia-tchouanc. **Mongolia:** no further data. **Korea (South):** Port Lazareff, 19.3 km from Gensan; Palgong San, 13 airline km N. of Taegu, 1200 m; Palgong San, 16 airline km N. of Taegu, 750 m.

**DISTRIBUTION** (Fig. 163, and Biogeography section, p. 163). Widely distributed in SE. Asia.

**BIOLOGY.** Little is known of the biology of this species. Adults are found from July to October. There are records of damage to citrus (Chen & Wong, 1936), rice (Cheo, 1937; Shiraki, 1952) and sugar cane (Butani, 1961; Box, 1953), the last from almost every country in which the insect is found. The records of rice damage in Taiwan (Box, 1953; Bei-Bienko & Mishchenko, 1951a; Cheo, 1937) have not been confirmed by examination of specimens during this study, though the species may be expected to occur there. Genetical studies of *O. infernalis* have been made by Lu (1951–2), Kawamura (1957), Takizawa & Narasawa (1971), and Inoue (1972). The Meloid beetle *Epicauta gorhami* was recorded as an egg predator in Japan (Nagatomi & Iwata, 1958).

**DISCUSSION.** At the commencement of this study there were two recognized subspecies of *O. infernalis*, and one closely related species, *O. manjius* Chang. All three taxa are here synonymized because the characters given by Chang (1939) and by Bei-Bienko & Mishchenko (1951b) cannot be considered sufficient to differentiate populations at species or subspecies level when comparative examination has been made of material from the whole range of the species.

*O. infernalis* was originally described from Japan. No locality was given but the species is known to extend from Kyushu island in the south to at least the central region of Honshu island in the north. Measurements for a series from Japan are given above (p. 129). The subspecies *O. infernalis amurensis* was a name coined by Ikonnikov for the unnamed variety '*O. infernalis* var?' from Amur described by Saussure (1884: 117). The varietal name *amurensis*, incorrectly attributed by him to Saussure, should therefore be considered as his own, as was correctly assumed by Bei-Bienko & Mishchenko (1951b: 577) when elevating the variety to subspecific status. However, because Ikonnikov attributed his name to Saussure he did not designate his material as types or place the words 'var. n.' after the name as he did elsewhere in the same paper when describing new taxa. In any case his material, originally housed in the 'Zoologisches Museum der Kais', Moscow University, is presumably lost. The unique male in Saussure's collection at Geneva is here regarded as the type and accordingly designated as the lectotype of *Oedaleus infernalis amurensis* Ikonnikov, 1911. Measurements of a series of specimens of both sexes from the type-locality are given above together with measurements of the lectotype (p. 129). Compared to Japanese specimens they are noticeably smaller though the ranges overlap. However, the shape, as judged by TL/PL and the length/depth ratio of the hind femur, is substantially identical.

*Oedaleus manjius* Chang, 1939 was described from material collected in Chekiang and Szechwan provinces of China. The measurements of a series collected at 1500 m in Szechwan and loaned to me by Dr A. B. Gurney (USNM, Washington) are given above (p. 130). The series was studied by Chang and one specimen (not measured) had been labelled '*Oedaleus wenchowensis* Chang, det. Chang 1936'. I am indebted to Dr Gurney for the following information:

'Chang's material, which had been borrowed here, was never returned from China, so that we do not have types or other material except what he named while in the United States, where he studied at Cornell University. In China he was at St. John's University, Shanghai, but whether anything of his remains there is unknown to us here. It is probable that he did not survive the war. My last word from him was in April 1939, at which time conditions there were very much upset. The name *Oedaleus wenchowensis* Chang which he placed on a label here in 1936 evidently applies to what he described in 1939 as *O. manjius*, the former just being a manuscript name of no permanent validity.'

Unfortunately Chang's diagnostic characters for *O. manjius* are unreliable since specimens from one locality exhibit great variation in minor details of the morphology of the head and pronotum and the colour of the hind tibiae and the ventral surface of the hind femora, all characters which he considered as conclusive in distinguishing his species from *O. infernalis*.

*Oedaleus infernalis montanus* Bei-Bienko, 1951 was described from material collected in 'Szechwan, Nan Shan Mts, and range of Burkhan-Budda'. The male only was described and distinguished by its author from other subspecies by the colour of the hind femora, by its small size, and by minute differences in the length of the 'median segments of antennae'. Of these characters only size is of any objective validity. The holotype was unavailable for study but the measurements of a

paratype from Lifan are given above. Bei-Bienko & Mischenko (1951b: 577) gave the range of tegmen length of the type-series as 16.5–20.0 mm though the specimen measured here is actually smaller than this. Measurements of two females from near Lifan are given for comparison. One of these is very large indeed, suggesting that the Himalayan population is not composed exclusively of dwarf individuals, though doubtless specimens caught at high altitude have a tendency to small size and relatively short tegmina and hind femora, a well-known phenomenon in montane Acridoidea (Uvarov, 1977: 436). Tegmen length of Bei-Bienko's series has an almost identical range to that of the specimens studied by Chang mentioned above and overall there is consistency within the material from south-west China. From the measurements given it is evident that the TL/PL ratio is different for both sexes of the Szechuan population compared to the L. Khanka population which is essentially lowland-living ( $\sigma$ :  $t = 6.03$ ,  $P < 0.01$ ;  $\text{♀}$ :  $t = 7.67$ ,  $P \ll 0.001$ ). A careful analysis of the effects of altitude on morphometrics in this species would be most interesting but at present there is no evidence of any genuinely geographically based variation worthy of subspecies status. In any case morphometric variation even within one population is so great that subspecies divisions based on only a few specimens from widely scattered localities are biologically meaningless.

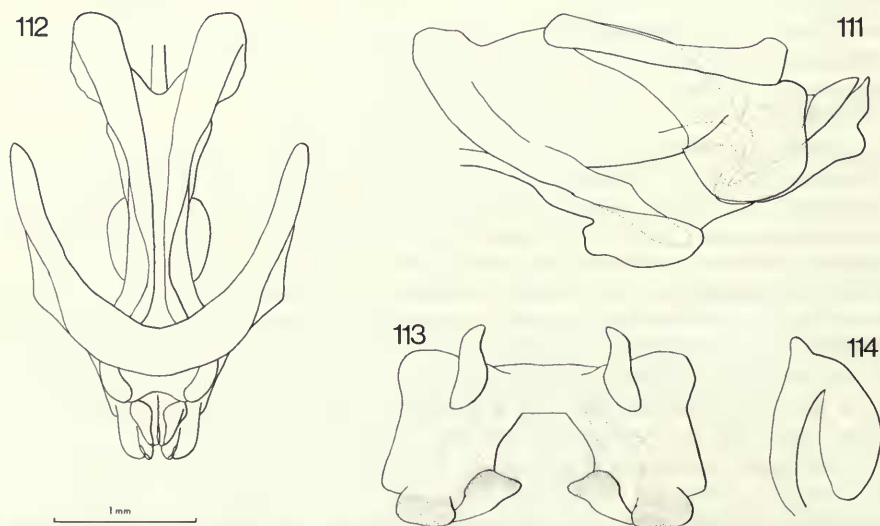
The original series of *O. infernalis* was stated by Saussure to be in Brunner's collection. There are today three specimens labelled as from Japan in the NM, Vienna. Of these the single male is designated as the lectotype, and the two accompanying females are designated as paralectotypes.

***Oedaleus formosanus* (Shiraki, 1910) comb. n.**

(Figs 7, 38, 53, 111–114, 163)

*Oedipoda formosana* Shiraki, 1910: 89. NEOTYPE  $\sigma$ , TAIWAN: Taikaizan (BMNH), here designated [examined].

$\sigma$ . Integument finely rugulose and sparsely hairy. Antennae about one and a third times as long as head and pronotum together, flagellum with 19 segments. Fastigium of vertex longer than wide, narrowing to half maximum width anteriorly, concave, with raised margins; frons in profile flat, frontal ridge narrowed just below vertex and again just below median ocellus. Eyes nearly one and a half times as deep as wide; genae sparsely hairy. Pronotum tectiform, finely rugose and pitted; median carina arcuate, intersected by posterior sulcus; lateral lobes of pronotum sparsely covered with long hairs; hind margin nearly rectangular; lateral surface of meso- and metathorax sparsely hairy. Tegmen surpassing folded hind knees by less than one-quarter of hind femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs about one and a half times as long as outer; apical tarsal segment three times as long as claw; arolium more than one third length of claw. Cerci



Figs 111–114 *O. formosanus*, genitalia. 111, endophallus and cingulum, lateral view; 112, same, dorsal view; 113, epiphallus; 114, spermatheca.



more than two and a half times as long as wide. Genitalia (Figs 111–113): cingular apodemes medium length, strongly curved, zygoma thickened; rami short, cingular and apical penis valves short, the latter with acute apices; subapical ventral process tumuliform; epiphallus long and broad with deeply arched bridge; lophi large, outer lobes wider than inner; anterior projections large, rounded, posterior projections rectangular.

General coloration brown, with darker brown markings. Head brown with oblique dark striations on genae and frons, vertex speckled. Pronotal X-marking forming a light area on shoulders of pronotum bounding dark medial area on dorsum; lateral surface of pronotum and meso- and metanotum with variable light and dark specks. Tegmen infusate brown throughout except for irregular pale triangle on costal margin one-third along from base and transparent specks in apical half visible when wing is open. Hind wing fascia (Fig. 7) complete and fusing posteriorly with infusate wing tip; basal area pale greenish yellow. Outer surface of hind femora with three oblique dark bands, inner surface with three transverse bands partially elided; interior ventral carina and ventral surface of hind femur scarlet; hind knees black; hind tibiae with thin black basal ring, otherwise coral to scarlet.

♀. Frons in profile convex. Ventral ovipositor valves (Fig. 53) narrow, almost triangular, strongly sclerotized, with curved apices. Spermatheca (Fig. 114) with apical diverticulum abruptly rounded apically, and with conical subapical diverticulum.

## MEASUREMENTS (all known specimens)

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25.82	3.94	4.89	18.2	12.91	2.98	4.35	3.71
Range	22.4–	3.6–	4.4–	15.6–	12.0–	2.4–	4.1–	3.5–
	29.6	4.5	5.5	20.9	14.4	3.3	5.0	4.0
S.D.	2.337	0.292	0.365	1.754	0.833	0.287	0.312	0.156
n	6	7	7	6	7	7	7	6

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	34.34	5.94	7.16	23.97	17.74	4.25	4.17	3.34
Range	29.8–	5.5–	6.5–	19.7–	15.9–	3.9–	3.8–	3.0
	41.0	6.7	8.6	29.3	20.9	4.8	4.3	3.4
S.D.	4.725	0.487	0.944	3.950	2.15	0.376	0.231	0.207
n	4	4	4	4	4	4	4	4

AFFINITIES. *O. formosanus* appears to be most closely allied to *O. infernalis*, but is quite distinct by virtue of its dark coloration and the extensive shading of the hind wing (Fig. 7), both features which are common to many high altitude oedipodine grasshoppers.

## MATERIAL EXAMINED

*Oedaleus formosanus* (Shiraki), neotype ♂, Taiwan: Taikeizan, 25.viii.1923 (Shiraki) (BMNH).

Taiwan: 1 ♀, Taikeizan, 25.viii.1923 (Shiraki) [labelled 'Oedaleus formosanus Shir. Cotyp.']; 1 ♂, 1 ♀, Daisuikutsu, 14.ix.1924 (Shiraki & Sonan) [♀ is labelled 'Oedaleus formosanus Shir. Cotyp.']; 2 ♀, Arisan, 2.vii.1947 (Gressitt) (CAS, San Francisco); 1 ♂, Arisan, 21.viii.1908 (ANS, Philadelphia); 3 ♂, Alishan, Chiayi Hsien, 1800 m, 11.ii–3.iii.1962 (Yoshimoto) (BPBM, Hawaii); 1 ♂, Arisan, 2130 m, 22.viii.1947 (Gressitt) (BPBM, Hawaii).

DISTRIBUTION (Fig. 163, and Biogeography section, p. 165). Known only from montane areas of Taiwan.

BIOLOGY. Unknown.

DISCUSSION. This species was not fully described by Shiraki (1910), probably as a result of an oversight, and it is known only from pl. 2, fig. 3 and the legend '*Oedipoda formosana* n. sp.'. In 1929, four specimens of this species were donated to the British Museum (Natural History) via the Commonwealth Institute of Entomology, and these were entered in the C.I.E. donations book on April 6th as four cotypes of *Oedaleus formosanus*. There are a number of problems posed by this

situation. Firstly, only the two females actually bear manuscript labels identifying them as cotypes, though it is probable that in his correspondence with C.I.E. Shiraki described them all as cotypes. This cannot now be verified since all pre-war C.I.E. correspondence was pulped during World War II. The second problem is that specimens collected several years after the publication of a species cannot possibly be cotypes (or, in modern usage, syntypes). It is conceivable that they were designated in a later publication, but if so this cannot now be traced. What is clear is that by 1929 Shiraki had realized that his species was an *Oedaleus* and he labelled the specimens he sent to C.I.E. accordingly. However, since no publication of this combination is known, it is here given as a new combination. Presumably Shiraki had specimens before him when writing his 1910 paper which he intended to designate as types but this material is now lost. Dr Syoziro Asahina has kindly checked Shiraki's collection at Hokkaido University, Sapporo, and he informs me that there is no named specimen of *Oedipoda formosana*. For this reason, and to establish the identity of the species, one male from Shiraki's later series is here designated as neotype.

***Oedaleus interruptus* (Kirby 1902)**  
(Figs 13, 26, 46, 115–118, 152)

*Chortoicetes interruptus* Kirby, 1902a: 232. LECTOTYPE ♂, SOUTH AFRICA: Transvaal (BMNH), here designated [examined].

*Oedaleus interruptus* (Kirby) Uvarov, 1925: 275.

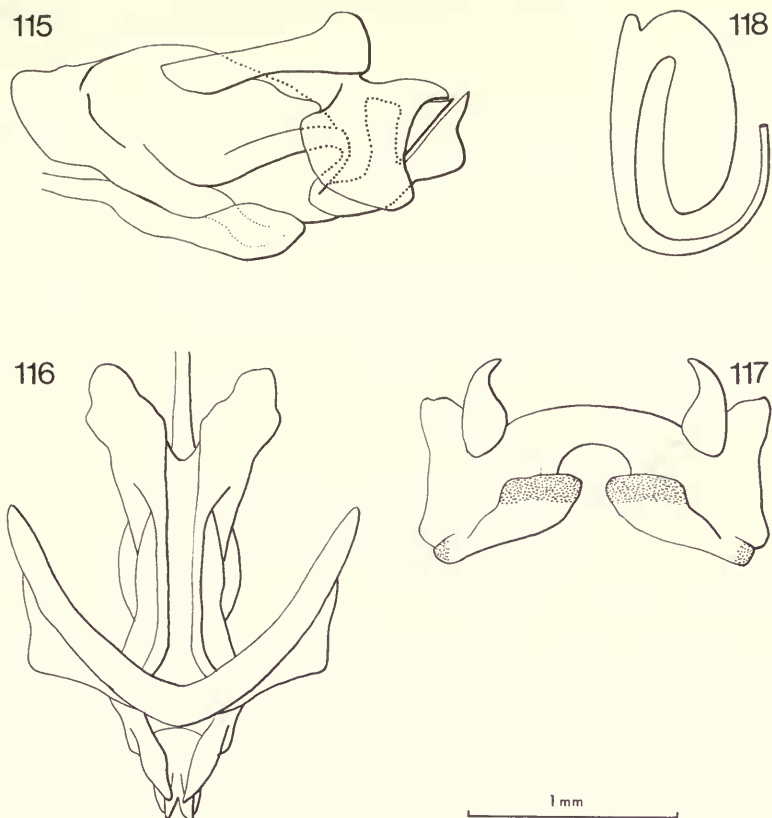
REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a quarter times as long as head and pronotum together; flagellum 20-segmented. Fastigium of vertex subtriangular, longer than wide with well-defined margins, narrowing anteriorly to one-third of maximum width. Frons in profile slightly convex. Frontal ridge slightly expanded dorsal to median ocellus, ventrally obsolescent. Eyes about one and a third times as deep as wide. Pronotum low tectiform, median carina arcuate, blade-like, not intersected by posterior sulcus. Posterior margin of pronotum acutangular to rectangular. Tegmen surpassing folded hind knees by one-fifth to one-third of hind femur length. Hind tibia with 11–12 inner and 11–13 outer spines. Inner apical spurs about one and a half times as long as outer. Apical tarsal segment about twice length of claw, arolium half length of claw. Cerci elongate, more than two and a half times as long as wide. Genitalia (Figs 115–117): cingular apodemes short, of medium thickness; rami long, slender; cingular and apical penis valves short, subapical ventral process large; epiphallus rectangular, bridge narrow, inner lobes of lophi three times as wide as outer lobes.

General coloration variable, brown, with lighter brown or green markings on vertex, frons, genae, pronotum, dorsal and lateral surface of folded tegmina and dorsal surface of hind femora. Pale X-marking of pronotum thin and distinct (♀ Fig. 26). Tegmen infuscate brown or brown and green in basal half with four pale transverse bands one-quarter, one-third, one-half, and three-fifths along from base; apical two-fifths clear with variable smoky patches. Hind wing fascia (Fig. 7) narrowly interrupted between second cubitus and first anal vein, or more widely, reaching margin of wing posteriorly; wing tip sometimes slightly infuscate, basal area of wing pale yellow. Hind femur with two transverse brown bands on external upper marginal area and one longitudinal brown streak on external medial area; ventral surface of hind femur suffused (often indistinctly) with rose pink. Hind tibia basally pale straw, otherwise brown suffused with pink. Hind knees brown or greenish.

♀. Ventral ovipositor valves (Fig. 46) moderately sclerotized, slender, Spermatheca (Fig. 118) with finger-like subapical diverticulum.

MEASUREMENTS (all available material)

		Males							
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL	
Mean	23.18	3.63	4.49	17.28	12.57	3.2	3.93	3.87	
Range	21.1–	3.3–	4.0–	15.4–	11.0–	2.8–	3.8–	3.5–	
	25.1	4.0	5.2	19.1	13.6	3.6	4.2	4.3	
S.D.	1.06	0.195	0.356	1.047	0.786	0.230	0.120	0.234	
n	9	11	10	11	10	10	10	10	



**Figs 115–118** *O. interruptus*, genitalia. 115, endophallus and cingulum, lateral view; 116, same, dorsal view; 117, epiphallus; 118, spermatheca.

Females

Mean	27.68	4.64	5.08	20.08	13.82	3.53	3.92	3.97
Range	25.1–	4.2–	4.1–	17.9–	12.6–	3.1–	3.8–	3.6–
	31.6	5.0	5.9	22.9	15.9	4.0	4.1	4.5
S.D.	2.052	0.240	0.430	1.566	0.998	0.267	0.111	0.262
n	12	13	12	13	12	12	12	12

**AFFINITIES.** *O. interruptus* is probably most closely related to *O. carvalhoi* with which it shares the characteristics of very fine X-markings on the pronotum, red hind tibiae and undersides of hind femora, and incomplete wing band. It is easily distinguished by its smaller and slenderer appearance and the acutely angled pronotal hind margin, an unusual feature in *Oedaleus*.

**MATERIAL EXAMINED**

*Chortoicetes interruptus* Kirby, lectotype ♂, **South Africa:** Transvaal, Pretoria (*Distant*) (BMNH).

**South Africa:** 1 ♂, 4 ♀, Transvaal, Pretoria (*Distant*) (including 1 ♀ paralectotype of *Chortoicetes interruptus* Kirby); 1 ♀, T., Krugersdorp, 22.xii.1902 (*Hamm*) (UM, Oxford); 1 ♂, T., Johannesburg (*Cregoe*); 1 ♂, Orange Free State, Harrismith, ii.1927 (*Turner*); 1 ♀, O.F.S., Gum Tree, ii.1932; 4 ♂, 9 ♀, O.F.S., Bloemfontein, 13.iv.1951 (*Botha*) (COPR, London); 1 ♀, Orange R. Colony (*B-Hamilton*); 1 ♂, 1 ♀, Cape Province, Grahamstown, 23.ii.1955 (*Greathead*); 2 ♂, C.P., Drakensburg Mts, Giant's Castle, 1957 (*Jago*); 1 ♀, C.P., 35.4 km W. of Cofimvaba, 940 m, 14.iv.1958 (*Ross & Leech*) (CAS, San Francisco); 1 ♀, C.P., Cape of Good Hope (*Brady*) (MHN, Geneva); 1 ♀, C.P., Cape of Good Hope (*Peringuey*) (MHN, Geneva); 1 ♂, 1 ♀, C.P., Bot River, xii.1930 (*Key*) (ANIC, Canberra).



DISTRIBUTION (Fig. 152, and Biogeography section, p. 156). Known only from eastern montane areas of South Africa.

BIOLOGY. Unknown. There is one report of damage to wheat at Bloemfontein (13.iv.51, *D. H. Botha*) recorded in the COPR collection index: 'The edges of the fields were severely damaged and in some cases had to be reploughed and resown. The fliers mostly roosted in grass outside the wheat fields and flew into them daily to feed on the green wheat'.

DISCUSSION. Kirby described *Chortoicetes interruptus* from material collected by Distant at Pretoria. Only one male and one female were referred to the new species. Kirby misidentified one further male and three females with identical data to the syntypes. Accordingly the single named male is designated lectotype and the female paralectotype. The remaining specimens are excluded from the paralectotype series.

***Oedaleus instillatus* Burr, 1900**  
(Figs 12, 33, 56, 119–123, 156)

*Oedaleus instillatus* Burr, 1900: 39. LECTOTYPE ♂, SOMALI REPUBLIC (UM, Oxford), here designated [examined].

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a quarter times as long as head and pronotum together; flagellum with 22 segments. Fastigium longer than wide, concave, narrowing to two-fifths of maximum width anteriorly; frons in profile slightly convex; frontal ridge slightly expanded at and narrowed below median ocellus. Eyes one and a third times as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin rectangular to acutangular. Tegmen surpassing folded hind knees by one-third to one-half of femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment two and a half times claw length; arolium two-fifths of claw length. Cercus one and four-fifths as long as wide. Genitalia (Figs 119–123): cingular apodemes of moderate thickness and curvature; rami fully developed with cingular and apical penis valves short; subapical ventral process large; epiphallus rectangular, inner and outer lobes of lophi small, subequal; anterior projections rounded, acute; posterior projections obtusangular.

General coloration variable, brown, with lighter brown (or, rarely, pale green) markings on frons, vertex, genae, pronotum, and dorsal surface of folded hind tegmina and hind femora. Tegmen infusate in basal two-thirds with three pale transverse bands situated one-third, one-half and two-thirds along from base, commencing from costal margin. Hind wing fascia (Fig. 12) complete, reaching hind margin of wing, basal area pale yellow, wing tip infusate. Hind femur with three oblique transverse bands on external medial and upper marginal areas; internal surface with basal pair of bands elided to form dark area; ventral surface pale red; hind knees dark brown, hind tibia with dark basal ring, thick subbasal pale area, otherwise pale red.

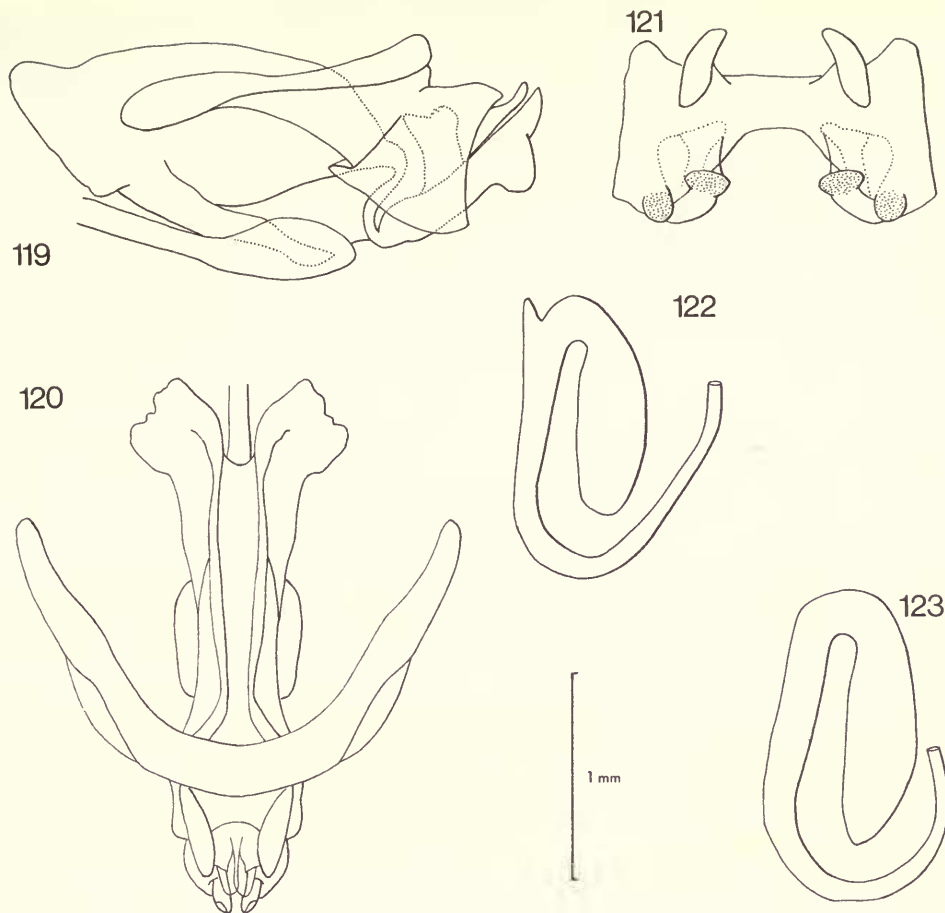
♀. Hind femur and tibia with very pale red pigment often appearing light brown. Ventral ovipositor valves (Fig. 56) elongate, moderately sclerotized, with exterior margin deeply incurved. Spermatheca (Fig. 122) with or without a short finger-like subapical diverticulum.

MEASUREMENTS

Sample from Kenya: El Wak, 2°47'N, 40°55'E, 5.xii.1944 (*Kevan*).

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	26.97	3.56	4.59	18.97	11.9	3.01	4.16	4.14
Range	23.8–	3.3–	4.2–	17.5–	11.2–	2.8–	3.7–	3.6–
	27.6	3.9	5.3	20.7	12.8	3.2	6.9	4.6
S.D.	7.045	0.142	0.287	0.82	0.411	0.125	0.795	0.259
n	28	29	26	29	14	14	14	25



**Figs 119–123** *O. instillatus*, genitalia. 119, endophallus and cingulum, lateral view; 120, same, dorsal view; 121, epiphallus; 122, spermatheca.

Females

Mean	32.61	4.90	5.77	24.11	15.15	3.83	3.95	4.20
Range	28.2–	4.3–	4.6–	22.0–	12.9–	3.3–	3.8–	3.6–
	37.3	5.8	6.9	27.4	18.0	4.5	4.1	4.7
S.D.	1.946	0.339	0.589	1.429	1.404	0.328	0.106	0.316
n	25	24	25	25	14	14	14	25

**AFFINITIES.** *O. instillatus* is allied to *O. roscens* and *O. obtusangulus* on the basis of its epiphallus morphology (Fig. 121), the lophi being small and of nearly equal size. It also shares with them its sombre coloration, green forms being relatively rare. This reflects the open dry habitats favoured by these species.

**MATERIAL EXAMINED**

*Oedaleus instillatus* Burr, lectotype ♂, **Somali Republic:** W. Somaliland, 16.iv.–7.viii.1895 (*Peel*) (UM, Oxford).

In addition to the lectotype, 468 specimens were examined from the following localities. **Somali Republic:** 1 ♀, W. Somaliland, 16.iv.–7.viii.1895 (*Peel*) (UM, Oxford) (paralectotype of *Oedaleus instillatus* Burr); Las Anod; Belet Uen; Debifrad; Adenival; 11.3 km N. of Bulu Burti; 9.7 km N. of Bulu Burti; nr Borama, 1350 m; 37 km N. of Borama, 10°03'N, 43°12'E; Hargeisa, locust camp; Hargeisa Tug; between Hargeisa

and Mendera; Derkengenyu; Mijertein, Domo; Ischia Baidoa; El Rago; Burao; El Afwein, N. Region; Wud Wud, 80.5 km NE. of Bohotle; between Mait and Las Khoreh, Haded Plain; Bohotleh; Welo, 09°28'N, 48°55'E; Afmadu; Haud, 8°29'N, 45°34'E, 750 m; N. Region, El Donfar, 10°40'N, 49°05'E; Hudin area, 09°10'N, 47°30'E; Erigavo scarp, 750 m; Mogadiscio, 5.vi.55; Bawn; Au Barre, 09°47'N, 43°13'E; Mijertein, nr Bender Beila. **Djibouti:** Dia forest, 64.4 km N. of Tadjura. **Ethiopia:** Ogaden, Wardere; Dire Daoua; Kobo; El Oha; Wallo, Yeju escarpment; Ogaden, nr Scillare; nr Ogaden, Argheile, 300 m, 05°10'N, 42°05'E; Dua Parma R., 1000 m; Erer Hotel; Harerge Province, Erer to Urso road, 12.1 km E. of Erer; Harerge Pr., 0.6 km E. of Erer, 1200 m. **Kenya:** El Wak, N.F.D.; Wajir distr., War Olia, 02°20'N, 40°33'E; Makindu; Voi; Machakos Hills; Samburu distr., Wamba, 00°58'N, 37°19'E; Madagheddi, Mendera distr., 03°43'N, 41°39'E; Mendera distr., Damassa, 03°09'N, 41°20'E; Kima; Magadi; Nairobi, Langata forest; 03°25'N, 40°12'E; Athi; Marsabit; Kindaruma, 00°47.5'S, 37°39.5'E; 6 km E. of Makutano, 02°31'S, 37°34.5'E; 16 km E of Makutano, 02°31'S, 37°40'E; Chyulu hills, 02°32'S, 37°46'E, 02°34'S, 37°49'E, 02°38.5'S, 37°51.5'E; Hola, 01°30'S, 40°00'E; Garissa to Thika, 00°47'S, 38°45'E; Selengai; Ulu; Samburu distr.; Giaxi, 00°01.5'N, 37°46'E; 9 km N. of Ishiara, 00°24.5'S, 37°51'E; Mt Marsabit, 7 km N. of Loglogu, 02°04'N, 37°54'E, 690 m; Meru National Park, 00°13'N, 38°05'E, 750 m; Meru Nat. Pk, 00°11'N, 38°04'E, 720 m; Meru Nat. Pk, site of old game lodge on Rojoweru R., 00°08'N, 38°16'E, 450 m; Meru Nat. Pk, 00°05'N, 38°16.5'E, 510 m; Meru Nat. Pk, Simba Lookout, 00°08'N, 38°09'E, 630 m; about 5 km W. of Ishiara town, 00°27'S, 37°45'E, 1050 m; approx. 3 km E. of Taru village, 03°45.5'S, 39°10'E, 330 m; 17 km NE. of Mambeala Rock, on road from Nguni to Kora, 00°20'S, 38°32'E, 540 m approx.; Mambeala Rock, road from Nguni to Kora, 00°26'S, 38°26'E, 720 m; 3 km SW. of Mambeala Rock, 00°27'S, 38°25'E, 720 m; Mt Marsabit, about 1 km from main road on short cut to L. Paradise, 02°16'N, 37°54'E, 1260 m; on road from Samburu to Marsabit, 101 km N. of Archer's Post, and 1 km S. of Merille R. bridge, 01°24'N, 37°43'E, 570 m; 17 km N. of Loglogu, at side of main road, 02°09'N, 37°53'E, 900 m; Salt Lick Lodge, 03°33'S, 38°13'E, 870 m; game area owned by Taita Hills Lodges, 03°32'S, 38°14'E, 900 m; Taita Hills Lookout, Mukiaio; Buffalo Springs Res., 00°33'N, 37°38'E, 15.vi.75; Ndetani, on road from Nguni to Kora (meeting place of five tracks), 00°35'S, 38°22'E, 720 m; Samburu distr., Varaguers Valley, E. of Wamba. **Tanzania:** Dodoma; Mkomasi station, 97 km W. of Amani; Kibwezi, Ukamba, 900 m; Meru, Nieder.

**DISTRIBUTION** (Fig. 156, and Biogeography section, p. 159). Widely distributed and common throughout the drier areas of eastern Africa.

**BIOLOGY.** Almost nothing is known of the biology of this common species. From label data it is apparent that adults may be seen at all times of the year. One hopper has been collected in January and one copulation observed in May. It is notable that specimens are rarest in March and July, both months of low rainfall, the latter also having lowest temperatures. Peak numbers have been collected in May and November, in each case one month after the two months of peak rainfall (Griffiths, 1972: 139). It is clear that there are at least two generations corresponding to these peaks and perhaps more in years of above-average rainfall. There is one record of night-flying 'swarms' of *O. instillatus* observed at El Wak in NE. Kenya, on 5.xii.1944 between 20.00 and 22.00 h (Kevan & Knipper, 1955: 312) but no details of density or behaviour were given. The measurements given are for a series from this swarm.

**DISCUSSION.** Burr described *O. instillatus* from one male and one female syntype. The male is here designated lectotype and the female paralectotype.

*Oedaleus obtusangulus* Uvarov, 1936

(Figs 3, 35, 55, 124–127, 156)

*Oedaleus obtusangulus* Uvarov, 1936: 542. Holotype ♀, SAUDI ARABIA (BMNH) [examined].

*Oedaleus villiersi* Chopard, 1950: 139. Holotype ♀, NIGER (MNHN, Paris) [examined]. **Syn. n.**

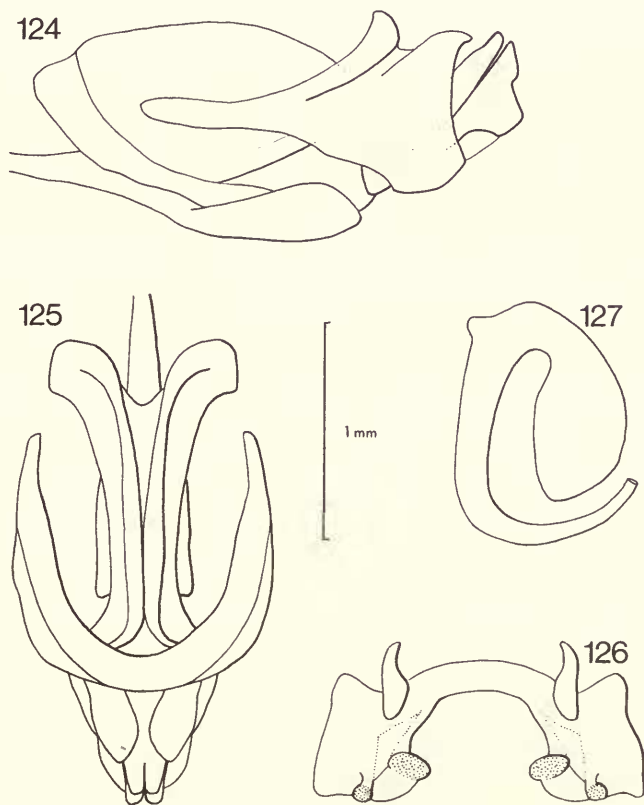
**REDESCRIPTION.** ♂. Integument finely rugulose and pitted. Antennae one and a third times as long as head and pronotum together, flagellum with 22 segments. Fastigium of vertex longer than wide narrowing to half maximum width anteriorly, concave with raised margins; frons in profile slightly convex; frontal ridge



constricted at vertex, slightly widened between antennal bases, constricted below median ocellus. Eyes one and a third times as deep as wide. Pronotum tectiform, rugose, with deep sulci; median carina arcuate, hind margin rectangular to obtusangular. Tegmen surpassing folded hind knees by one-half to one-third of length of hind femur. Hind tibia with 11 inner and 10–11 outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice length of claw; arolium less than half length of claw. Cerci twice as long as basal width. Genitalia (Figs 124–126): cingular apodemes long, strongly curved; rami well developed; cingular and apical penis valves short; subapical ventral process large; epiphallus elongate trapezoidal with thin arched bridge; inner lobes of lophi small, twice as wide as outer lobes; anterior projections large, rounded acutangular; posterior projections smaller, rounded acutangular.

General coloration greyish brown with lighter markings on frons, genae, pronotum, tegmina and hind femora. Tegmen infusate in basal half, with two irregular pale transverse bands extending from costal margin, first band one-third along from base, reaching at least to subcostal vein, sometimes to second cubitus posteriorly; second band half way along wing, reaching first cubitus posteriorly. Apical third of tegmen clear with variable degree of infusate speckling. Hind wing fascia (Fig. 3) variable in emphasis, widely but variably interrupted around first cubitus, reaching hind margin of wing posteriorly; basal area pale yellow or colourless. Hind femur with three variable transverse markings on external and internal upper marginal area extending indistinctly obliquely forward across external medial area; inner and ventral surfaces of hind femur straw-coloured; hind tibia with dark basal ring, subbasal pale area, otherwise straw-coloured.

♀. Ventral ovipositor valves (Fig. 55) elongate, weakly sclerotized, laterally excavated; basivalvular sclerite smooth. Spermatheca (Fig. 127) with short rounded apical diverticulum and very short subapical diverticulum.



Figs 124–127 *O. obtusangulus*, genitalia. 124, endophallus and cingulum, lateral view; 125, same, dorsal view; 126, epiphallus; 127, spermatheca.

## MEASUREMENTS

Sample from Saudi Arabia: various localities.

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	21.52	3.32	3.85	15.62	10.08	2.72	3.71	4.08
Range	18.6–24.0	2.9–3.5	3.5–4.3	13.7–17.5	9.1–11.6	2.2–3.1	3.5–4.0	3.6–4.6
S.D.	1.339	0.171	0.280	1.007	0.672	0.202	0.123	0.269
n	20	21	21	20	21	21	21	20

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	28.43	4.62	5.21	20.44	13.61	3.59	3.79	3.93
Range	25.2–32.9	4.1–5.3	4.6–6.1	18.1–23.9	11.9–15.5	3.1–4.0	3.5–4.1	3.6–4.3
S.D.	2.079	0.381	0.393	1.474	0.976	0.236	0.147	0.164
n	16	16	16	16	16	16	16	16

Sample from Niger: Air (all available material of '*villiersi*').

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
♂	23.1	3.4	4.2	17.0	10.9	2.8	3.8	4.1
Paratype ♂	22.0	3.2	3.8	16.4	9.7	2.8	3.5	4.3
Paratype ♂	23.8	3.4	4.1	17.8	10.4	2.7	3.8	4.3
Paratype ♀	28.7	4.8	5.4	20.9	13.4	3.8	3.5	3.9
Holotype ♀	28.1	4.6	5.2	20.4	13.6	3.6	3.7	3.9

AFFINITIES. *O. obtusangulus* is most closely allied to *O. instillatus* and *O. roscens* on the basis of general shape and colour and in particular the morphology of the epiphallus, which in all three species has small inner and outer lobes of equal size.

## MATERIAL EXAMINED

*Oedaleus obtusangulus* Uvarov, holotype ♀, Saudi Arabia: Buraiman, 17.ii.1929 (*Philby*) (BMNH). *Oedaleus villiersi* Chopard, holotype ♀, Niger: Air, Tésuar, viii.1947 (*Chopard*) (MNHN, Paris).

**Saudi Arabia:** 3 ♂, 2 ♀, Asir, Wadi Hali, 18°45'N, 41°55'E, 300 km, 9–10.i.1948 (*Popov*); 1 ♂, 1 ♀, Wadi Harub, 17°10'N, 42°50'E, 1.i.1947 (*Popov*); 1 ♀, Wadi Jowra, 17°15'N, 43°00'E, 30.xii.1946 (*Popov*); 1 ♀, Lahawash, foothills NE. of Sabiya, 150–240 m, 18.i.1950 (*Tillin*); 1 ♂, Buraiman, nr Jeddah, 17.i.1947 (*Popov*); 1 ♂, Hawi valley, 20.v.1936 (*Philby*); 6 ♂, 3 ♀, Lodar, 800 m, 16.v.1967 (*Guichard*); 2 ♂, Seil el Kebir, 23.iii.1969 (*Popov*); 1 ♂, Aqiq-Baha, crops, 3.vi.1969 (*Popov*); 1 ♀, Baha, 7.vi.1969 (*Popov*); 1 ♀, 2 nymphs, Aqiq, 2.vi.1969 (*Popov*); 3 ♂, 2 ♀, Hada, *Acacia* bush, 1700 m, 4.v.1969 (*Popov*); 1 ♀, Upper Wadi Alahsiba, Tihama, 10.ii.1962 (*Popov*); 1 ♂, Sab[i]ya, 17°10'N, 72°40'E, iii.1945 (*Waterston*). **Yemen:** 1 ♀, Hodeidah, locust research station [actual site of collection unknown]. **Niger:** 1 ♂, Tarrowadji, 900 m, viii.1947 (*Chopard*) (MNHN, Paris); 2 ♂, Air, Irabellaben, ix.1947 (including allotype ♂ of *Oedaleus villiersi* Chopard) (MNHN, Paris); 1 ♂, Air, 100 km N. of Agadez towards In Guezzam, 25.viii.1967 (*Popov*).

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). This species has a relict montane distribution in the western Sahara and south-west Arabia.

BIOLOGY. Unknown.

DISCUSSION. The measurements given above indicate that the few known specimens of *O. villiersi* fall well within the range of size of *O. obtusangulus*. In all other respects the two separated

populations appear to be morphologically identical. Chopard was probably unaware of the Arabian species previously described by Uvarov when he described *O. villiersi*.

*Oedaleus rosescens* Uvarov, 1942

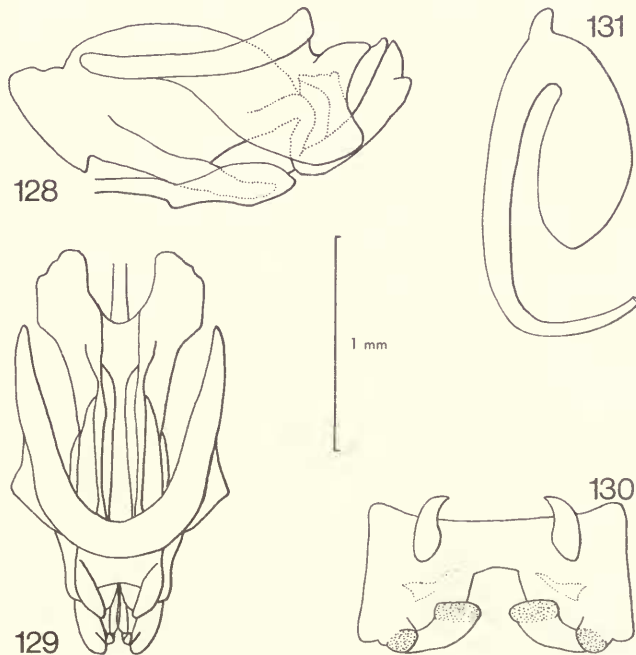
(Figs 4, 31, 54, 128–131, 157)

*Oedaleus rosescens* Uvarov, 1942: 582. Holotype ♂, INDIA (BMNH) [examined].

REDESCRIPTION. ♂. Integument finely rugulose and pitted. Antennae one and a half times as long as head and pronotum together; flagellum with 22 segments. Fastigium of vertex much longer than wide, concave, narrowing to about half of maximum width anteriorly, with well-defined margins; frons in profile convex; frontal ridge slightly expanded at median ocellus. Eyes 1.3 times as deep as wide. Pronotum low tectiform; median carina arcuate, barely intersected by posterior sulcus; hind margin obtusangular. Tegmen surpassing hind knees by about one-third of hind femur length. Hind tibia with 10 outer and 11 inner spines; inner apical spurs one and a half times as long as outer; apical tarsal segment twice claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs 128–130): cingular apodemes long and strongly curved; rami well developed with short cingular valves and apical penis valves; subapical ventral process small; epiphallus rectangular with narrow thick straight bridge angled within; inner lobes of lophi one and a half times wider than outer lobes; ancorae small; anterior and posterior projections rounded rectangular.

General coloration reddish brown with lighter brown markings on frons, genae, pronotum, tegmina and hind femora. Tegmen infuscate brown in basal half, with irregular pale transverse band extending from costal margin to first cubitus posteriorly, situated one-third along from base, second transverse band reaching first cubitus about half way along wing; apical third of tegmen clear with variable brown speckling. Hind wing fascia (Fig. 4) complete, slightly sigmoid, reaching hind margin of wing; basal area of wing pale pink. Hind femur with three indistinct transverse dark markings on external upper marginal area. Internal lateral surface of hind femur black in basal half with black transverse band one-third back from apex; ventral surface of hind femur pink, hind knee internally black; hind tibia with dark basal ring, subbasal pale area, otherwise pale pink.

♀. Ventral ovipositor valves (Fig. 54) short with strongly curved apices. Spermatheca (Fig. 131) with apical diverticulum rounded, with short subapical diverticulum.



Figs 128–131 *O. rosescens*, genitalia. 128, endophallus and cingulum, lateral view; 129, same, dorsal view; 130, epiphallus; 131, spermatheca.



## MEASUREMENTS (all available specimens)

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	22.2	3.24	3.63	16.31	10.39	2.94	3.55	4.47
Range	20.6–24.0	3.0–3.6	3.4–4.0	15.2–17.9	9.7–11.2	2.6–3.2	3.5–3.7	4.3–4.6
S.D.	1.202	0.178	0.213	0.912	0.516	0.177	0.09	0.083
n	8	8	7	8	8	8	8	7

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27.96	4.41	4.77	20.46	13.37	3.79	3.53	4.31
Range	25.9–29.2	4.0–4.7	4.4–5.0	18.6–21.8	12.4–14.0	3.4–4.0	3.36–3.69	4.06–4.69
S.D.	1.154	0.218	0.202	1.083	0.647	0.212	0.125	0.204
n	7	8	8	7	8	8	8	7

AFFINITIES. *O. rosescens* is most closely allied to *O. instillatus* and *O. obtusangulus* on the basis of general shape and coloration and more specifically the epiphallus shape (Fig. 130). It is, however, quite distinct by virtue of the continuous fascia (Fig. 4) and pink basal area of the hind wing.

## MATERIAL EXAMINED

*Oedaleus rosescens* Uvarov, holotype ♂, India: Rajasthan, Nokh, 1.viii.1937 (BMNH).

India: 4 ♂, 4 ♀, nr Bikaner, Udransar, 20.viii.1963 (*Popov*); 2 ♀, nr Bikaner, viii.1963 (*Popov*); 1 ♂, Rajasthan, nr Barmer, Cho[h]tan, 26.viii.1959 (*Flower*); 1 ♀, Rajasthan, Jaisalmer [Jaisalmer], sandy hillsides with coarse grass, 8.ix.1959 (*Flower*); 1 ♂, Rajasthan, Jodhpur, 15.ix.1959 (*Flower*). Pakistan: 1 ♀, Khewra, Salt Range, from green grass and green trees, 24.ix–x.1930 (*Hora & Pruthi*) (paratype of *Oedaleus rosescens* Uvarov); 1 ♂, Landhi, on grass, 7.x.1975 (*Bashir*).

DISTRIBUTION (Fig. 157, and Biogeography section, p. 163). NW. India and NE. Pakistan.

BIOLOGY. Unknown.

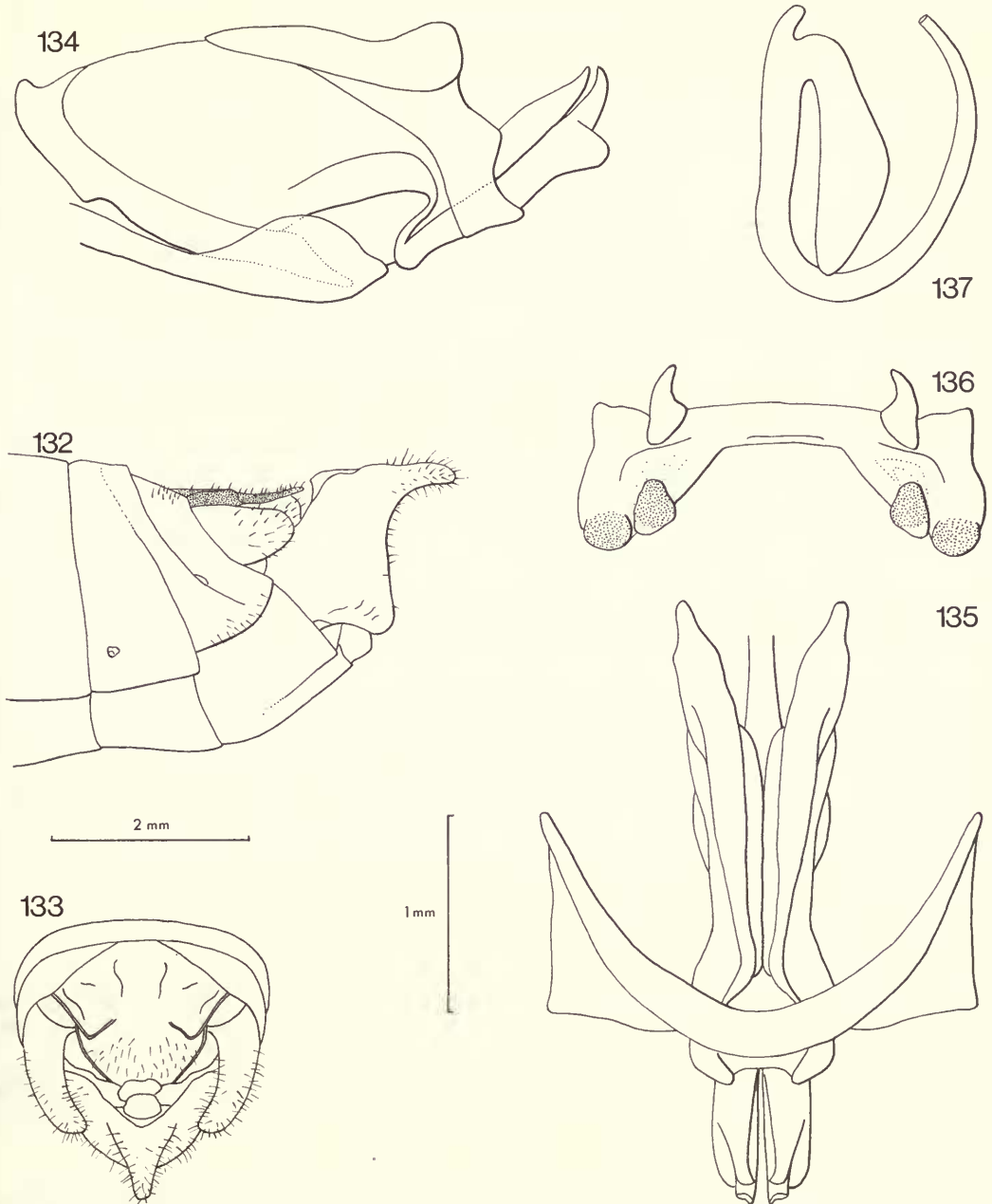
*Oedaleus miniatus* Uvarov, 1930  
(Figs 16, 32, 59, 132–137, 156)

*Oedaleus miniatus* Uvarov, 1930a: 177. Holotype ♀, SOMALI REPUBLIC (BMNH) [examined].

♂. Integument rugose and wrinkled. Antennae slightly longer than head and pronotum together, distinctly flattened, ensiform; flagellum with 22 segments. Fastigium of vertex longer than wide, concave, with well-defined lateral carinae, narrowing to one-third of maximum width anteriorly; frons in profile flat or slightly concave with projecting angle between frons and vertex; frontal ridge strongly narrowed just ventral to fastigium, expanded at and slightly constricted ventral to median ocellus. Eyes about one and a half times as long as wide. Pronotum tectiform, strongly rugose; median carina arcuate, intersected by posterior sulcus; anterior arms of pronotal X-marking placed on narrow raised ridges; hind margin acutangular to rectangular. Tegmen surpassing folded hind knees by one-third of length of hind femur. Hind tibia with 11–13 spines inside and out; inner apical spurs about twice as long as outer; apical tarsal segment twice length of claw; arolium less than one-third length of claw. Cerci twice as long as basal width; subgenital plate with an acute dorsal posterior process (Figs 132, 133). Genitalia (Figs 132–136): cingular apodemes short, thin crescent-shaped, obtusely curved; rami short, reduced, with apices of cingular valves and apical penis valves long and exposed, the latter with acute flattened chisel-like tip and pronounced subapical ventral processes; epiphallus short and wide, with broad, thin, flat bridge, lophi with inner and outer lobes small and nearly of equal size; ancorae small; anterior projections small, rectangular; posterior projections obsolete.

General coloration variable, brown, with lighter brown or green markings on frons, vertex, genae and pronotum. Eyes with four light vertical stripes sometimes visible in anterior half (Fig. 32). Tegmen infuscate brown in basal half with irregular pale transverse band on costal margin, reaching second anal vein posteriorly, situated one-third along from base, continuous when folded with light band on hind femur;

secondary light band between half and two-thirds along from base sometimes visible. Hind wing fascia (Fig. 16) complete, angled at dividing vein, spreading towards base and tip of wing along costal margin, basal area of wing bright scarlet, apical portion of wing slightly clouded. Outer surface of hind femora with three oblique transverse dark bands separated by lighter areas; interior surface with three transverse brown bands partially elided; interior ventral carina and ventral surface of hind femur orange-red; hind knees blackish, tibiae with incomplete narrow dark basal ring, subbasal wide pale ring, otherwise orange-red.



**Figs 132–137** *O. miniatus*, genitalia. 132, apex of male abdomen, lateral view; 133, same, dorsal view; 134, endophallus and cingulum, lateral view; 135, same, dorsal view; 136, epiphallus; 137, spermatheca.

♀. Frons in profile concave to convex; head large. Pronotum rugose, warty. Tegmen shorter, just surpassing hind knees, narrowing towards apex; costal margin subbasally expanded. Hind wing scarlet, faded to salmon pink in some specimens, with dark fascia almost obsolete on small specimens. Hind femora with interior ventral carina suffused with orange-red; hind tibiae orange. Ventral ovipositor valves (Fig. 59) with weakly sclerotized apices. Spermatheca (Fig. 137) with apical diverticulum tapering proximally and distally, and with short finger-like subapical diverticulum.

## MEASUREMENTS

Sample from Kenya: Hola, 1°30'S, 40°00'E (*I. A. D. Robertson*).

## Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	25.67	3.88	5.26	18.36	12.47	3.63	3.44	3.51
Range	23.3–27.9	3.5–4.4	4.5–6.2	16.6–20.1	10.9–14.0	3.1–4.1	3.3–3.8	3.1–3.8
S.D.	1.465	0.265	0.534	1.078	0.884	0.272	0.126	0.219
n	10	11	11	10	11	11	11	10

## Females

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	28.1	6.08	7.1	18.29	15.01	4.58	3.28	2.58
Range	26.4–29.2	5.7–6.5	6.7–7.6	17.2–19.0	14.4–16.0	4.4–4.8	3.1–3.5	2.5–2.7
S.D.	1.267	0.309	0.382	0.763	0.621	0.168	0.156	0.097
n	5	5	5	5	5	5	5	5

AFFINITIES. *O. miniatus* is most closely allied to *O. nadiæ*, under which species the principal similarities and differences are discussed. The unique features of this species include the very wide epiphallus (Fig. 136) and the curiously elongated subgenital plate (Figs 132, 133). The female possesses the least sclerotized ovipositor valves of any member of the genus, which suggests some ecological difference in oviposition between this species and its near relatives. Conceivably egg pods are deposited among the roots of vegetation clumps rather than in the more resistant soil. This, however, is merely a hypothesis. The small equal-sized lobes of the epiphallal lophi suggest a tenuous link between *O. miniatus* and *O. nadiæ* on the one hand, and the *obtusangulus-rosescens-instillatus*-group on the other. However, it is clear that *O. miniatus* has undergone a long period of evolutionary divergence from the main stem of *Oedaleus*.

Uvarov (1930a: 177) felt that *O. miniatus* might merit a separate genus, but incorrectly allied it to *O. carvalhoi*, to which it is not closely related. With the discovery of *O. nadiæ*, an intermediate species between *O. miniatus* and the rest of the genus, there seems less reason to erect a new genus for the latter.

## MATERIAL EXAMINED

*Oedaleus miniatus* Uvarov, holotype ♀, **Somali Republic**: Shimba Beris, Surud range, 10°54'N, 47°12'E, 2025 m, 17.xii.1929 (BMNH).

**Somali Republic**: 1 ♀, Beles Gogani, 01°30'N, 41°40'E, 30.ix–6.xii.1954 (*Greathead*). **Kenya**: Hola (Galole), Tana R. distr., 01°30'S, 40°00'E, 70 m, 11.vii.1972 (*Robertson*); 10 ♂, 5 ♀, same data, 29.xii.1972.

DISTRIBUTION (Fig. 156, and Biogeography section, p. 159). Known only from the Somali Republic and Kenya.

BIOLOGY. Unknown.

DISCUSSION. The original description of *O. miniatus* by Uvarov (1930a: 177) was based on a single female specimen collected at 2025 m in the Surud Range of N. Somalia. More recently specimens have been collected in southern Somalia and in Kenya which are much larger, with the hind wing fascia better developed. A close comparison with the holotype is no longer possible since



it has been reduced by insect damage to a shell consisting of the pronotum, tegmina, hind wings and left mid leg. However, all the known specimens appear to belong to one species, though further collecting in northern Somalia may demonstrate that the population from which the holotype came is a montane relict which has diverged sufficiently from the main population of the species further south to be considered as a separate subspecies. The male of this species, previously unknown, is here described for the first time.

*Oedaleus nadiae* sp. n.  
(Figs 30, 58, 138–141, 156)

♂. Integument rugose and wrinkled. Antennae slightly longer than head and pronotum together. Flagellum 20-segmented. Fastigium of vertex longer than wide, subtriangular, concave, with well-defined margin; frons in profile slightly convex, almost straight; frontal ridge strongly narrowed just below fastigium and with a slight constriction just ventral to median ocellus. Eyes about one and a half times as deep as wide. Pronotum tectiform, strongly rugose, median carina arcuate, intersected by posterior sulcus; anterior arms of pronotal X-marking placed on raised ridges; hind margin acutangular; mesosternal interspace anteriorly narrower than metasternal but wider posteriorly. Tegmen surpassing folded hind knees by one-tenth to one-third of hind femur length; tibia with 10 outer and 11–12 inner spines; inner apical spurs nearly twice as long as outer; apical tarsal segment twice claw length; arolium about half claw length. Cerci length twice basal width. Genitalia (Figs 138–140): cingular apodemes medium length, evenly tapering; rami short, apices of cingular and apical penis valves long and exposed, the latter with acute chisel-like apices and pronounced lobular subapical ventral process. Epiphallus trapezoidal with lateral plates indented; bridge flat and thick, lophi with inner and outer lobes subequal in size. Anterior projections large, rectangular, posterior projections rectangular.

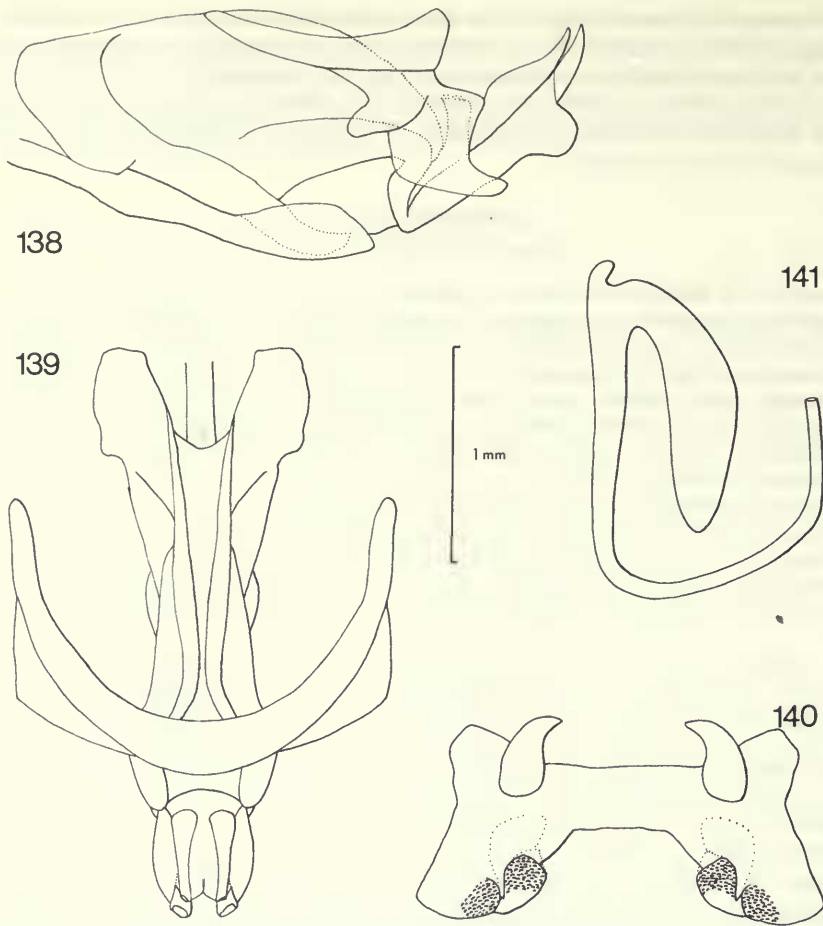
General coloration mottled brown with light brown or green markings on frons, vertex, genae and pronotum. Eyes with four light vertical stripes sometimes visible in anterior half. Broad pale pronotal X-marking (Fig. 58) sometimes continuous posteriorly with pale band fringing hind margin of pronotum. Tegmen infusate brown in basal two-thirds with two pale transverse bands reaching to first anal vein posteriorly; apical third of tegmen clear, with dark speckles. Hind wing lacking fascia, with pale crimson basal area and darkened main veins. Outer surface of hind femora with three oblique dark bands separated by lighter areas; internal surface with dark brown medial area; interior ventral carina orange; hind knees blackish, tibiae orange.

♀. Antennae 22-segmented. Pronotum heavily rugose, warty. Ovipositor valves pale with weakly sclerotized excurved apices (Fig. 58). Spermatheca (Fig. 141) with apical diverticulum elongated, tapering, and with short finger-like subapical diverticulum.

MEASUREMENTS (all known specimens)

		Males						
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	23.68	3.96	4.78	16.88	11.83	3.53	3.35	3.54
Range	21.6–25.4	3.6–4.2	4.3–5.4	15.4–18.5	10.6–12.6	3.2–3.9	3.3–3.5	3.2–4.0
S.D.	1.252	0.170	0.314	1.04	0.725	0.207	0.085	0.276
n	8	8	8	8	8	8	8	8
		Females						
Mean	31.96	6.05	7.18	22.05	15.41	4.53	3.41	3.10
Range	27.4–36.5	5.4–6.7	6.0–8.6	18.5–25.5	12.7–17.9	3.7–5.3	3.2–4.0	2.8–3.4
S.D.	2.835	0.472	0.840	2.067	1.556	0.547	0.173	0.161
n	16	17	17	16	17	17	17	16

AFFINITIES. *O. nadiae* is most closely allied to *O. miniatus*. Principal characters in common are the general shape (rather stocky in the female), red hind wing, short cingular rami with exposed



Figs 138–141 *O. nadiae*, genitalia. 138, endophallus and cingulum, lateral view; 139, same, dorsal view; 140, epiphallus; 141, spermatheca.

cingular and apical penis valves with very large subapical ventral processes (Fig. 138), and inner and outer lobes of epiphallic lophi small and nearly equal in size. The principal differences are that *O. nadiae* has an unbanded hind wing, a less elongated epiphallus, and the male subgenital plate not produced into a sharp point.

#### MATERIAL EXAMINED

Holotype ♂, **Somali Republic**: between Hargeisa and Mandera, 7.vi.1955 (*Uvarov*) (BMNH).

Paratypes. **Somali Republic**: between Hargeisa and Mandera, 7.vi.1955 (*Uvarov*); 1 ♀, El Rago, 8.xii.1953 (*Popov*); 4 ♀, Las Anod, 1935 (*Peck*); 2 ♂, 2 ♀, same data, 16.xi.1935; 1 ♂, 2 ♀, Ainabo, 8.vi.1952 (*Popov*); 2 ♀, 40 km WNW. of Borama, Aubube, 25.v.1958 (*Hussein*); 1 ♂, 17.7 km NW. of Borama, 7.vi.1957 (*Roffey*); 1 ♂, 1 ♀, Gardo plain, nr Hargeisa, 23.v.1967 (*Yussuf*); 2 ♂, N. region, between Mait and Las Khoreh, 20.v.1967 (*Yussuf*); 2 ♀, El Donfar, 10°40'N, 49°05'E, 22.v.1967 (*Yussuf*).

**DISTRIBUTION** (Fig. 156, and Biogeography section, p. 159). This species is known only from the northern region of Somalia.

**BIOLOGY**. Unknown.

**DISCUSSION**. This species is named in honour of Dr Nadia Waloff.

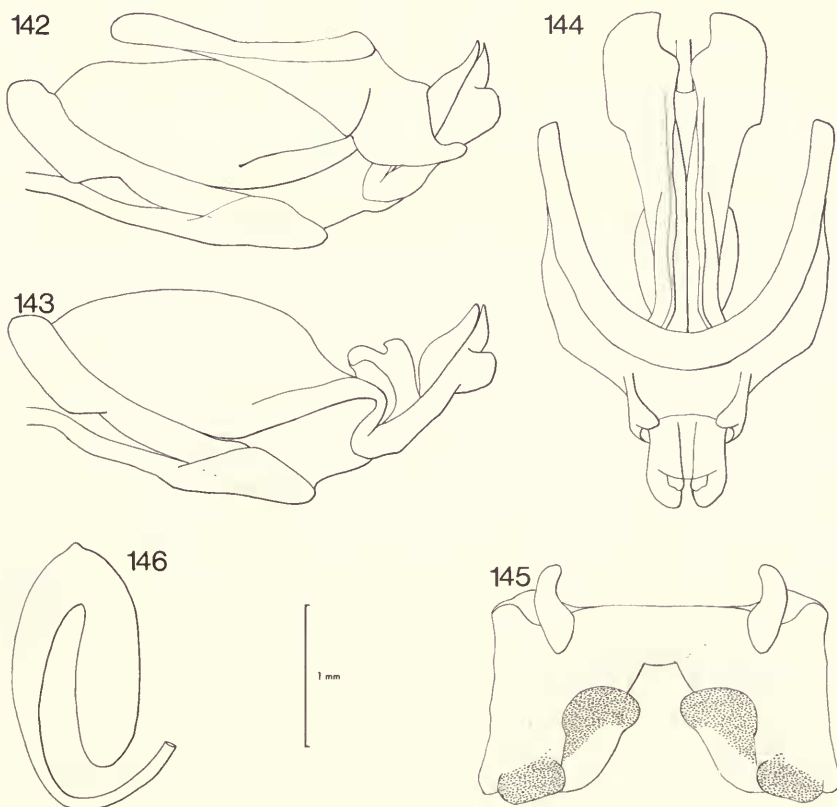
*Oedaleus inornatus* Schulthess-Schindler, 1898

(Figs 25, 57, 142–146, 156)

*Oedaleus inornatus* Schulthess-Schindler, 1898: 27. Holotype ♀, SOMALI REPUBLIC: Dolo, viii.1893 (*E. Ruspoli*) (MCSN, Genoa).

REDESCRIPTION. ♂. Integument rugulose and pitted. Antennae one and one-third times as long as head and pronotum together, flagellum 22- to 23-segmented. Fastigium longer than wide, shallowly concave, narrowing to half maximum width anteriorly, margins only slightly raised; frons in profile slightly convex; frontal ridge slightly expanded above median ocellus. Eyes one and two-fifths as deep as wide. Pronotum tectiform; median carina arcuate, not intersected by posterior sulcus; hind margin obtusangular. Tegmen surpassing folded hind knees by one-quarter to one-third of hind femur length. Hind tibia with 13 inner and 11–12 outer spines; inner apical spurs about one and one-third times as long as outer; apical tarsal segment nearly twice claw length; arolium half claw length. Cerci twice as long as basal width. Genitalia (Figs 142–145): cingular apodemes long and of moderate thickness and curvature; rami short, cingular and apical penis valves protruding strongly; subapical ventral process large; epiphallus rectangular, bridge thick, narrow, lophi very large and heavily sclerotized, inner lobes larger than outer; anterior and posterior projections lobate, acutely rounded.

General coloration brown, with light brown or green markings on vertex, frons, genae, pronotum, and dorsal surface of folded tegmina and hind femora; green forms relatively rare. Tegmen infusate brown in basal half with three variable transverse bars or blotches situated one-sixth, one-third, and one-half of distance along from base; apical half clear with variable brown patches. Hind wing without fascia but with infusate wing tip, and occasionally, faint traces of fascia near hind margin; basal area pale yellow. Hind femur with three variable oblique dark bands on outer medial and upper marginal areas, basal pair of bands



Figs 142–146 *O. inornatus*, genitalia. 142, endophallus and cingulum, lateral view; 143, same, cingulum removed; 144, endophallus and cingulum, dorsal view; 145, epiphallus; 146, spermatheca.



elided on inner surface to form large black area; ventral surface scarlet; hind knees black, hind tibia with narrow dark basal ring and broad pale subbasal area, otherwise scarlet.

♀. Hind femora and tibiae less distinctly red than male. Ventral ovipositor valves (Fig. 57) elongate triangular, well sclerotized, with smoothly incurved exterior margins. Spermatheca (Fig. 146) with apical diverticulum vestigial.

#### MEASUREMENTS

Sample from Somali Republic: various localities.

Males								
	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	33.16	5.11	6.08	23.88	17.14	4.36	3.93	3.92
Range	27.4–37.3	4.4–5.7	5.2–6.8	19.5–27.0	15.1–19.3	3.5–4.9	3.7–4.1	3.6–4.2
S.D.	3.658	0.453	0.528	2.754	1.63	0.40	0.157	0.207
n	12	12	12	12	12	12	12	12
Females								
Mean	43.16	6.98	7.83	30.82	21.12	5.3	3.99	3.91
Range	33.6–48.9	6.2–7.9	6.4–9.3	23.6–35.2	16.7–25.3	4.3–6.1	3.8–4.4	3.5–4.5
S.D.	4.57	0.556	0.766	3.357	2.155	0.508	0.156	0.271
n	18	19	19	18	19	19	19	18

**AFFINITIES.** *inornatus* is characterized by the total absence of a wing band and by the very robust genitalia, in particular the epiphallus with its very large lophi. It is impossible to relate this species to the others with any degree of certainty. It may possibly be an offshoot of the *senegalensis*-group.

#### MATERIAL EXAMINED

**Somali Republic:** 2 ♂, 4 ♀, northern region, between Mait and Las Khoreh, 20.v.1967 (Yussuf); 2 ♂, Gardo plain, nr Hargeisa, 23.v.1967 (Yussuf); 4 ♂, 4 ♀, Haded plain, 24.v.1967 (Yussuf); 1 ♂, Burao area, 27.v.1967 (Yussuf); 1 ♂, Las Khoreh, 21.v.1967 (Yussuf); 1 ♂, 08°15'N, 47°50'E, 24.xi.1946 (Wood); 3 ♀, El Donfar, 10°40'N, 49°05'E, 22.v.1967 (Yussuf); 1 ♀, Las Anod, 1935 (Peck); 1 ♂, 1 ♀, same data, xi.1935; 1 ♀, same data, 8.i.1936; 2 ♂, same data, 16.xi.1935; 1 ♀, Derkengenyu, 21.xi.1935 (Peck); 1 ♀, Bul Beali, 08°15'N, 47°50'E, 24.xi.1946 (Wood); 2 ♀, Dan Gudban hills, 08°15'N, 47°15'E, 24.xi.1947 (Wood); 1 ♀, Borama, 1500 m, 13.vi.1952 (Popov). **Ethiopia:** 4 ♂, 2 ♀, Mega, Borama, x.1951 (Bellehu); 1 ♀, Harerge pr., Melka Werer, Inst. Agr. Res., 14.5 km ENE. of station, grassland pasture, 30.ix.1975 (Jago) (MA, Addis Ababa). **Kenya:** 6 ♂, 9 ♀, on Emali – Chyulu Hills road, 6 km E. of Makutano, flat plain, grass with *Acacia* trees, 02°31'S, 37°34.5'E, 1050 m, 1972 (Robertson); 2 ♂, Emali – Makutano – Chyulu Hills road, 16 km E. of Makutano, roadside, short open grass plains just W. of Elmau Hill, c. 1100 m, 02°31'S, 37°40'E, 1972 (Robertson); 1 ♀, Lesai area, 29 km SE. of Korondil, Moyale dist., 02°55'N, 39°15'E, thorn bush, 15.vi.1946 (Kevan); 1 ♀, Chopu Gof, Marsabit, 02°25'N, 38°03'E, grass and scrubby bushes, 13.vi.1946 (Kevan); same data, 29.ii.1944; 1 ♀, Wajir dist., Well Marer, 02°05'N, 40°30'E, desert grass and thorn bush, 21.vi.1944 (Kevan); 1 ♀, N.F.D., El Wak, desert grass, thorn bush, 5.xii.1944 (Kevan); 1 ♀, same data, 25.v.1944; 1 ♂, 4 ♀, 17 km N. of Loglogu, at side of main road, 02°09'N, 37°53'E, 900 m, 19.v.1975 (Robertson) (COPR, London); 1 ♂, nr Ferguson's Gulf, L. Turkana, hillside nr hill called Luola, 03°24'N, 35°49'E, 16 km along new road to Lodwar, 540 m, 4.vii.1975 (Robertson) (COPR, London); 1 ♀, Ferguson's Gulf, L. Turkana, Angling Lodge, 03°33'N, 35°56'E, 370 m, 3.v.1975 (Robertson) (COPR, London).

**DISTRIBUTION** (Fig. 156, and Biogeography section, p. 159). Widely distributed but not common throughout the drier areas of north-eastern Africa.

**BIOLOGY.** Unknown. A gynandromorph specimen of this species has been described (Ritchie, 1978b).

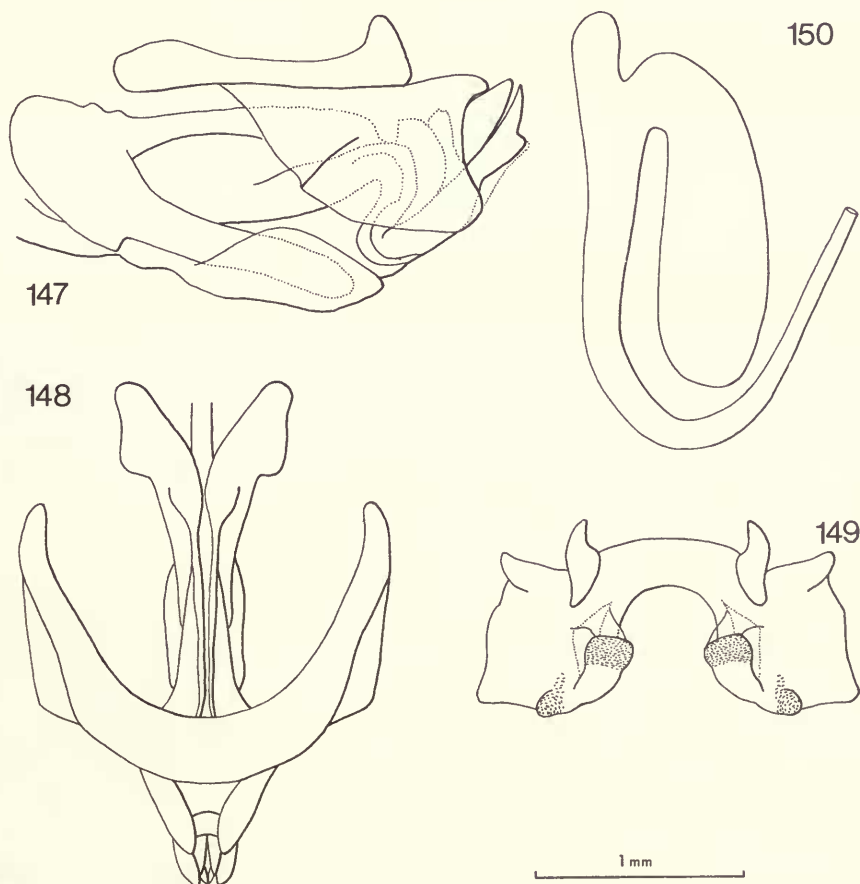
*Oedaleus flavus* (Linnaeus, 1758)  
(Figs 17, 34, 49, 50, 147–150, 155)

*Gryllus Locusta flavus* Linnaeus, 1758: 433.

This species is here divided into two subspecies under which the specific synonyms are separately listed below.

REDESCRIPTION. ♂. Integument finely rugose and warty. Antennae slightly longer than head and pronotum together, flagellum with 22 segments. Fastigium longer than wide, widest medially, tapering both anteriorly and posteriorly, concave, with well-defined margins; frons in profile convex; frontal ridge almost parallel-sided, slightly divergent between antennal bases. Eyes about one and two-fifths times as long as wide. Pronotum tectiform with sparse warts, at least in prozona; median carina arcuate, intersected by posterior sulcus; hind margin of pronotum acutangular. Tegmen surpassing folded hind knees by about one-fifth to one-third of hind femur length. Hind tibia with 12 inner and outer spines; inner apical spurs one and a half times as long as outer; apical tarsal segment one and four-fifths length of claw; arolium less than half claw length. Cerci two and a half times as long as basal width. Genitalia (Figs 147–149): cingular apodemes medium length, medially thickened; rami slender, elongate, cingular valves and apical penis valves short; subapical ventral process small; epiphallus trapezoidal, lateral plates slightly excurved; bridge arched, thick; lophi with inner lobes larger than outer; anterior projections small, acutely rounded; posterior projections rectangular, rounded.

General coloration dark brown, with lighter brown (or rarely green) markings on frons, vertex, genae, and



Figs 147–150 *O. flavus*, genitalia. 147, endophallus and cingulum, lateral view; 148, same, dorsal view; 149, epiphallus; 150, spermatheca.

pronotum. Tegmen infuscate brown in basal two-thirds with three pale transverse bars at intervals of one-quarter, one-half, and two-thirds along from base; apical third clear with brown speckles. Hind wing fascia (Fig. 17) complete, continued half way towards apex of wing between first radial vein and radial sector; wing tip variably infuscate; basal area of wing bright opaque lemon-yellow. Outer surface of hind femora with three oblique dark bands; hind knees blackish, hind tibiae orange-red.

♀. Dorsal surface of pronotum with large warts and posterior arms of X-marking very thick (Fig. 34). Hind wing tip not clouded. Ovipositor valves strongly sclerotized and excurved. Spermatheca (Fig. 150) with apical diverticulum bulbous, preapical diverticulum stout.

AFFINITIES. *O. flavus* is probably allied to *O. instillatus* on the basis of its epiphallus having small lophi (Fig. 149) and the same characteristic suggests a link with *O. plenus* with which it may be confused on superficial examination. The bright yellow basal area of the hind wing is, however, a sufficient diagnostic character.

DISTRIBUTION (Fig. 155, and Biogeography section, p. 157). Widely distributed in eastern and southern Africa with a broad discontinuity corresponding with the *Brachystegia* woodland zone.

BIOLOGY. Little is known of the biology of this species. It was reported by Ballard (1914) as a pest of tobacco in Malawi. Phipps (1959) recorded mean numbers of 35.0 and 36.8 ovarioles per female in two samples of two and four specimens respectively in Tanzania. The chromosomes have been briefly discussed by Nolte (1939).

The two subspecies of *O. flavus* may be separated by the following keys.

#### Males

- 1 Interior surface of hind femur with one transverse and one U-shaped dark band, not intersecting the internal ventro-lateral carina; basal half of interior surface, internal ventro-lateral carina, and ventral surface suffused with red (East Africa) . . . . . *O. flavus somaliensis* (Sjöstedt) (p. 152)
- Interior surface of hind femur with dark bands enlarged and crossing internal ventro-lateral carina onto ventral surface; central portion of interior surface suffused with mauve or black, never red (South Africa) . . . . . *O. flavus flavus* (Linnaeus) (p. 150)

#### Females

- 1 Ventral surface of hind femur, particularly internal ventro-lateral carina, suffused with red, sometimes discoloured, never black; basivalvular sclerite of ventral ovipositor valves smooth (Fig. 50) . . . . . *O. flavus somaliensis* (Sjöstedt) (p. 152)
- Ventral surface of hind femur, particularly in inner half, suffused with black, never red; basivalvular sclerite of ventral ovipositor valves with raised warts in posterior half (Fig. 49) . . . . . *O. flavus flavus* (Linnaeus) (p. 150)

### *Oedaleus flavus flavus* (Linnaeus, 1758)

*Gryllus Locusta flavus* Linnaeus, 1758: 433. Lectotype ♀, AFRICA (ZIUU, Uppsala), designated by Dirsh (1961: 317) [not in LS, London, as stated by Dirsh, *op. cit.*] [examined].

*Gryllus flavus* (Linnaeus) Fabricius, 1775: 292 [locality: Piedmont, indicates partial confusion with *Oedaleus decorus* (Germar)].

*Acrydium flavum* (Linnaeus) Olivier, 1791: 227. [Incorrectly gives *Acrydium nigrofasciatum* Degeer, 1773 as synonym.]

*Gryllus flavus* (Linnaeus) Petagna, 1792: 319. [Incorrectly gives *Acrydium nigrofasciatum* Degeer as synonym.]

*Oedipoda flava* (Linnaeus) Serville, 1831: 288.

*Oedipoda flava* (Linnaeus); Burmeister, 1838: 643. [Incorrectly gives *Acrydium nigrofasciatum* Degeer as synonym.]

*Pachytylus (Oedaleus) flavus* (Linnaeus) Stål, 1873: 125.

*Humbella flava* (Linnaeus) Saussure, 1884: 107.

*Oedaleus nigrofasciatus* var. *citrinus* Saussure, 1888: 41. LECTOTYPE ♂, SOUTH AFRICA: 'Cap.' (MHN, Geneva), here designated [examined]. [Synonymized by Dirsh, 1961a: 317.]

*Oedalus* (sic) *citrinus* (Saussure); Distant, 1892: 260.

*Oedaleus citrinus* (Saussure); Kirby, 1910: 225.

*Oedaleus flavus* (Linnaeus) Kirby, 1902a: 73. [Incorrectly gives *Oedaleus nigrofasciatus* Degeer as synonym.]

*Humbe flava* (Linnaeus) Kirby, 1910: 215.

*Oedaleus flavus* (Linnaeus); Dirsh, 1961a: 317. [Reinstates original usage.]

#### MEASUREMENTS

Sample from South Africa: various localities.

#### Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	28.19	4.27	5.45	20.99	13.92	3.71	3.75	3.85
Range	26.4–	3.9–	5.1–	19.6–	12.9–	3.3–	3.6–	3.7–
	29.9	4.7	5.9	22.4	15.2	4.2	4.0	4.0
S.D.	1.212	0.206	0.228	1.041	0.762	0.264	0.126	0.093
n	11	11	11	11	11	11	11	11

#### Females

Mean	37.0	5.79	7.04	27.58	17.78	4.93	3.61	3.93
Range	34.8–	5.0–	6.3–	26.0–	16.1–	4.3–	3.4–	3.7–
	39.9	6.3	7.8	29.5	19.4	5.2	3.8	4.3
S.D.	1.537	0.346	0.402	1.015	0.844	0.277	0.114	0.165
n	11	11	11	11	11	11	11	11

#### MATERIAL EXAMINED

*Gryllus Locusta flavus* Linnaeus, lectotype ♀, **Africa**: no further data (ZIUU, Uppsala). *Oedaleus nigrofasciatus* var. *citrinus* Saussure, lectotype ♂, **South Africa**: Cape of Good Hope, no further data (MHN, Geneva).

In addition to the lectotypes, 94 specimens were examined from the following localities. **Angola**: Tundavala, 13–16 km NW. of Sa da Bandeira, 14°50'S, 13°25'E, 1800–2100 m. **Zimbabwe**: Gwanda, 900m; Odzi distr., Zimbabwe, 1050–1440m; Matopo Hills; Shangani, De Beers ranch; nr Salisbury, Bindura. **Mozambique**: Malongotiba; Namaacha; Matola Rio; Umbeluzi; Inolabane. **Namibia**: Oshikango, 1100 m; 21 km NW. of Oshakati, Ovamboland; Otjangasema, Kaokoveld N. **Botswana**: 4.8 km NE. of Maun; Bathoon dam, Kanye; Mogobane; Metsimaklaba. **South Africa**: Transvaal, Louis Trichardt; T., Zoutpansberg; T., Pretoria; T., N. of Nelspruit; T., Tom Burke, 23°04'S, 28°00'E; T., R Limpopo, 23°00'S, 27°57'E; T., Kruger National Park, 16 km NE. of Skukuza; T., Klaserie Nature area, Klaserie R; T., 28 km E. of Barberton, 510m; T., Barberton; Natal, 16km N. of Ubombo, 160m; 4.8 km N. of Ubombo, 300m; N., Pietermaritzburg; N., Zululand, Lower Umfolosi R.; N., Durban; N., Klipfontein; Cape Province, 35.4 km W. of Cofimvaba, 940 m; C.P., 13 km S. of Balfour, 500 m; C.P., Grahamstown; C.P., Katberg, 1200 m; C.P., Fish R. valley; C.P., 32 km ENE. of Bredasdorp, Kars (Salt) R.; C.P., 32 km SE. of Swellendam; C.P., Zuurberg Pass, 24 km N. of Addo; C.P., Oakhill, 48 km NE. of Port Elizabeth; C.P., Capetown; C.P., De Hoop Vlei, 32 km E. of Bredasdorp; C.P., Cape of Good Hope; C.P., Resolution, Ft Brown.

**DISCUSSION.** The male specimen of *O. nigrofasciatus* var. *citrinus* here designated as lectotype bears a label in Saussure's hand: '*citrinus* Sss. ♀ [incorrect sex] Cap. Type'. The status of six female specimens in the collection is unclear and they have accordingly not been designated as paralectotypes.



*Oedaleus flavus somaliensis* (Sjöstedt, 1931) comb. et stat. n.*Gastrimargus somaliensis* Sjöstedt, 1931b: 26. Holotype ♀, SOMALI REPUBLIC (NR, Stockholm) [examined].

## MEASUREMENTS

Sample from Kenya: various localities.

Males

	Total length	Head width	Pronotum length	Tegmen length	Femur length	Femur depth	FL/FD	TL/PL
Mean	27.4	4.11	5.12	20.56	13.45	3.59	3.74	4.03
Range	24.7–29.3	3.7–4.5	4.5–5.6	18.5–22.2	11.6–15.1	3.3–4.0	3.4–4.0	3.6–4.5
S.D.	1.216	0.217	0.303	1.004	0.865	0.183	0.136	0.231
n	22	22	22	22	22	22	22	22

Females

Mean	38.74	6.18	7.1	29.08	18.49	5.11	3.62	4.10
Range	33.3–45.6	5.5–6.5	6.1–7.8	24.7–34.4	15.7–21.6	4.5–5.7	3.4–3.8	3.8–4.5
S.D.	2.752	0.385	0.472	2.147	1.294	0.324	0.130	0.208
n	14	14	13	14	14	14	14	13

## MATERIAL EXAMINED

*Gastrimargus somaliensis* Sjöstedt, holotype ♀, **Somali Republic**: Alessandra, Chismaio, 1928 (*Kinell*) (NR, Stockholm).

In addition to the holotype, 88 specimens were examined from the following localities. **Somali Republic**: nr Afmadu; Iscia Baidoa; S. Region, 11.3 km N. of Bulu Burti; Mogadiscio. **Kenya**: Hola (Galole), 01°30'S, 40°00'E, 70 m; Tana R. Distr., Hola (Galole), 01°25'S, 39°57'E, less than 100 m, 20 km N. of Hola on Garsen to Garissa road; 30 km S. of Hola on Garsen to Malindi road, 01°47'S, 40°02'E, 45 m; 85 km N. of Malindi, on Malindi to Garsen road, 02°28'S, 40°08'E, 30 m; 80 km W. of Malindi, on Malindi – Sala – Tsavo road, 03°06'S, 39°22'E, 150 km; N. F. D., Moyale; Ngong; Ngong forest; Athi Plains; Garsen; Turkana, Kacheliba; Mida Creek, Kilifi distr., 03°19'S, 39°58'E, sea level; approx. 3 km E. of Taru village, 03°45.5'S, 39°10'E, 330 m; Lukenia Hill, 35 km from Nairobi, on Mombasa road, site about 3.2 km along side road, 01°29'S, 37°04'E, 1740 m. **Uganda**: Moroto; Kidepo National Park, Kidepo valley, approx. 03°55'N, 33°50'E; Karamoja. **Sudan**: Mongalla; Juba, Mongalla. **Tanzania**: Morogoro distr., Mikumi; Kilosa; Rukwa Rift, Moomba R.; Usasi, clearings, 72.5 km NW. of Singida; Old Shinyanga; Samui, nr Manyon R., S. of Shinyanga; Tinde; 32 km SW. of Shinyanga; Tindiga; Mikumi; Mlingano, Ngomeni.

**DISCUSSION.** *Gastrimargus somaliensis* Sjöstedt (1931b) is here considered as a subspecies or geographical race of *O. flavus*. The external morphology and male genitalia of the two forms are identical apart from the minor differences detailed in the key above (p. 150). Despite these consistent differences the overall shape and size of the animals has remained remarkably constant in the two disjunct populations. Tegmen length is slightly significantly ( $P < 0.05$ ) larger in East African females than in South African, but in males there is no significant difference. Pronotum length is significantly smaller ( $P < 0.002$ ) in East African males than South African, but in females there is no significant difference. The TL/PL ratio is significantly higher in East African specimens ( $P < 0.01$  ♂,  $< 0.05$  ♀) and the sexual dimorphism as measured by mean  $T♀/T♂$  (Farrow, 1972) is greater in the former (1.414) than the latter (1.314).

The present interrupted distribution of the two races probably resulted from the recent interposition of the *Brachystegia* woodland across a previously continuous range of savannah (Van Zinderen Bakker, 1976). As described above (p. 156) *O. plenus plenus* also has two populations separated by the woodland, but without having undergone any apparent morphological divergence. For this reason and in view of the small amount of divergence which can be observed in the two populations of *O. flavus*, the process of speciation is considered to be incomplete.

## Biogeography of the genus *Oedaleus*

### Relationships within the genus

The genus *Oedaleus* comprises a homogeneous group of oedipodine grasshoppers colonizing a wide range of grassland habitats throughout the tropical and warmer temperate regions of the Old World. Before any analysis of the influences that have shaped the present distribution of the genus can be attempted it is necessary to describe the groupings of species which can be made on morphological grounds. These are tabulated below.

Group I	Group II
<i>O. senegalensis</i>	<i>O. instillatus</i>
<i>O. nigrofasciatus</i>	<i>O. obtusangulus</i>
<i>O. australis</i>	<i>O. roscens</i>
<i>O. abruptus</i>	
<i>O. virgula</i>	Group III
<i>O. johnstoni</i>	<i>O. miniatus</i>
<i>O. nigeriensis</i>	<i>O. nadiae</i>
<i>O. carvalhoi</i>	
<i>O. plenus</i>	Ungrouped species
<i>O. decorus</i>	<i>O. inornatus</i>
<i>O. infernalis</i>	<i>O. flavus</i>
<i>O. formosanus</i>	
<i>O. interruptus</i>	

Group I are linked by the possession of the following combination of characters: 1, similar genitalia having epiphallic lophi with unequal sized lobes; 2, the basal area of the hind wing pale yellow; 3, smooth integument with pronounced green-brown polymorphism. *O. interruptus* is unusual in having a strongly acutangular hind margin to the pronotum, but is otherwise a member of this group. Group II have the epiphallus almost square with small, equal sized lobes to the lophi. Group III have pink wings and rugose integument and are probably closely related although each species has peculiarities which suggest that they have been genetically isolated one from the other over a long period. *O. roscens*, another species with pink wings, is placed in group II since it resembles the other two species of that group in all other characters.

### Geographical origin of the genus

Analysis of the existing distribution of the genus strongly suggests an origin within the Ethiopian Region. The evidence for this can be summarized as follows.

1. The species endemic to Africa show the greatest range of interspecific morphological diversity, whereas those outside Africa can be placed in one or other of the African groups of species.
2. More than half of the known species (13) are found in Africa south of the Sahara. One other is known from North Africa and yet another species is endemic to Madagascar.
3. The genera most closely related to *Oedaleus* are either endemic to the Ethiopian Region (e.g. *Humbe* Bolívar, *Oreacris* Bolívar, *Locustana* Uvarov), or are Malagasian (e.g. *Pycnocrania* Uvarov), or are at least well represented in Africa (e.g. *Locusta* Linnaeus, *Gastrimargus*).

La Greca (1970) has drawn attention to the danger of assuming an Ethiopian origin for groups which may have entered Africa from southern Europe or western Asia, and whose present distribution may represent a relic of a much more extensive fossil or prehistoric range which would have included those areas. He cites the examples of the lion and the rhinoceros whose present limited distribution has been reduced largely by human activity. As to the savannah grasshoppers, however, it seems improbable that anything short of major habitat degradation would have brought about multiple extinctions. In Australia some flightless members of the endemic subfamily Morabinae are reported to survive only in graveyards and other refuges where sheep grazing is prevented (Key, 1974). However, *Oedaleus* together with several other Oedipodines is able to survive under a wide range of ecological conditions, largely because of its effective egg diapause

and the high mobility of the adults. For these reasons an African origin, or at least a primary radiation within Africa, seems most probable. To gain some idea of the forces which could have brought about the present day radiation of species it is necessary to examine some of the major features, past and present, of the African biomes.

### The Pleistocene in Africa

Moreau (1966), in his study of the bird faunas of Africa, has reviewed the climatic changes of the Pleistocene in Africa, and has presented strong circumstantial evidence for his belief that the forces that have shaped the avian fauna have, for the most part, operated within the last 70 000 years. At present there is no coherent chronological scheme that would harmonize all the known geological changes which have occurred in different parts of Africa within that period of time. However, it is possible to date some Pleistocene features in Africa and to relate them to events both in different parts of Africa itself and in Europe.

The two major influences on vegetation in the past have been changes in temperature and humidity and the most significant fluctuations in both have been associated with glaciation. As well as a direct lowering of temperature, glaciation has a complex effect on atmospheric circulation which in turn causes changes in the rainfall pattern which are the subject of opposed theories. In the last one million years there have been four glaciations, each with a similar temperature minimum and each separated by an interglacial period with higher peak temperatures than at present. The course of the last glaciation is better known than that of the previous ones and serves as a model in considering some of the dramatic changes which have repeatedly affected both the climate and vegetation of Africa. There is, however, the important reservation that human influence has been much more significant since the last glaciation than at any earlier period.

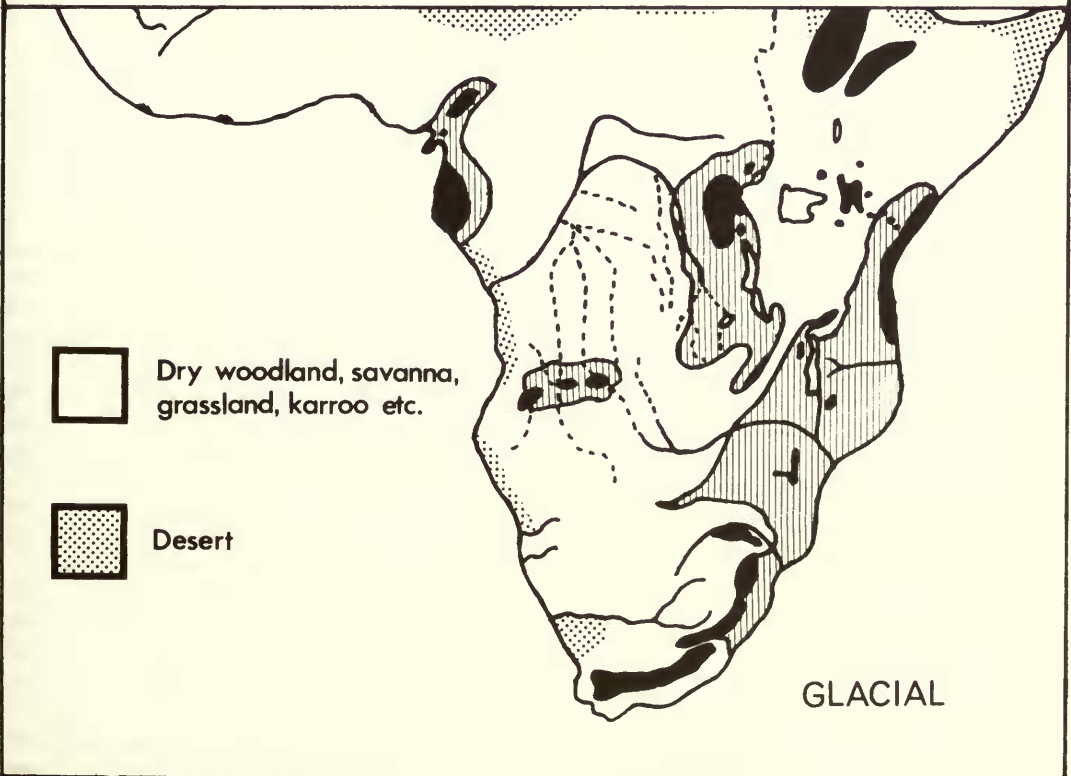
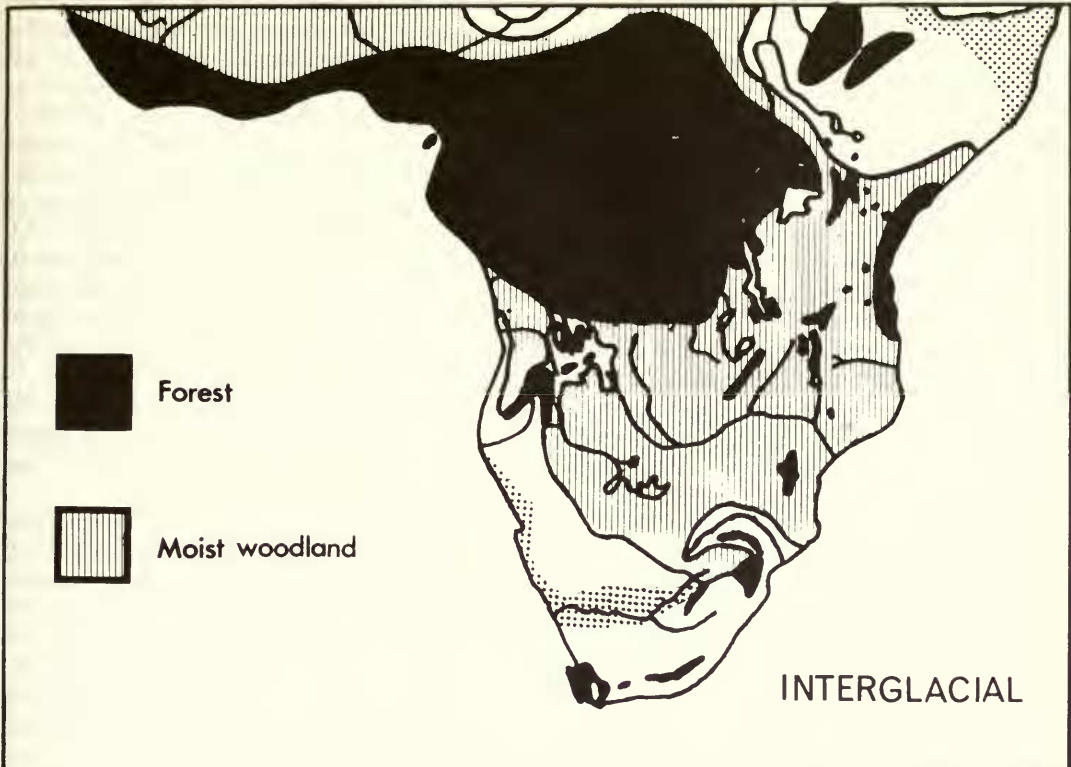
The last glaciation began around 70 000 years B.P. (before present), and its last severe stage lasted from 25 000–15 000 B.P. with a peak at 19 000 correlated with arctic conditions in central Europe. From around 16 000 B.P. the temperature rose very sharply except for brief cold relapses around 10 500 B.P. and again between 5500 and 4700 B.P. (Van Zinderen Bakker, 1969*a*). Present temperatures were reached around 8000 B.P., then exceeded by as much as 2°C around 6000 B.P. Finally, between 1400 and 1850 AD temperatures were slightly lower than now (Moreau, 1966). These cyclical temperature changes, which are presumed to be of cosmic origin, have exercised a profound effect on plant and animal distribution patterns both directly and through their influence on precipitation, evaporation and ocean currents. The results of this influence are discussed below on a regional basis in relation to the distribution of the species of the genus *Oedaleus*.

### The southern African *Oedaleus* fauna

According to Moreau (1966), the most stable parts of Africa during the Pleistocene have been the Namib and Kalahari deserts of southern Africa and the Somali peninsula of eastern Africa. Van Zinderen Bakker (1975) has reviewed evidence relating to the age, origins and movements of the Namib and Kalahari and concludes that they originated in the Oligocene about 40–45 million years B.P. At glacial maxima these deserts have enlarged and moved northwards in response to the growth of the polar ice-cap and the attendant shift towards the equator of the climatic belts and cold upwelling at the convergence of the Benguela and Angola currents on the west coast of southern Africa. Other effects of glaciation would have included decreased precipitation from colder oceanic water and an increase in the incidence of violent winds (Van Zinderen Bakker, 1976), both of which would have an aridifying influence. Successive enlargements of the Kalahari have pushed the *Brachystegia* woodland and the lowland forest zones back towards the equator, at the same time dissecting them into a number of separate refuges. Van Zinderen Bakker (1976) has produced tentative vegetation maps of Africa south of the Sahara during a glacial and an interglacial maximum showing how open savannah and dry grassland would have increased in extent, offering contact between eastern and southern Africa for the semi-arid biota including *Oedaleus* (Fig. 151). Conditions at the height of the last glaciation would have provided an

Fig. 151 Tentative vegetation maps of Africa south of the Sahara during a glacial and an interglacial maximum (simplified from Van Zinderen Bakker, 1976).







opportunity, perhaps the most recent of several, for species of the east African savannah and semi-arid zones to mix with those occupying similar habitats south of the equator, and vice versa, in the temporary absence of the woodland barrier which is at present more than 500 miles wide. At the same time much of South Africa and Botswana would have deteriorated from *Acacia* grassland to desert or near desert. The montane grassland of southern Transvaal, Orange Free State, Lesotho, and south-east Cape Province would have descended as much as 1000 metres but would apparently have suffered no reduction in area and may have constituted a relatively stable habitat during the Pleistocene. Certainly *O. interruptus*, the most distinct of the southern African species, is restricted to this habitat (Fig. 152) though apparently not found above about 2500 m. *O. nigrofasciatus*, another southern species, also favours the montane grassland (Fig. 152), whereas *O. carvalhoi* does not occur there (Fig. 152) although both species are found together further north and west across the *Acacia* and 'Mopane' wooded savannah. Both species bear a marked similarity to species found to the north of the *Brachystegia* belt. *O. nigrofasciatus* is morphologically almost indistinguishable from *O. senegalensis*, while *O. carvalhoi* shows a strong resemblance to *O. nigeriensis*. It is probable that these and other southern species and subspecies have been able to evolve in isolation from northern populations because of the periodic fragmentation of the humid woodland barrier described above. The importance of this barrier in the development of the African biota and the evidence in favour of it are discussed below (p. 171).

The two subspecies of *O. plenus*, a southern African species (Fig. 153), have a geographically and ecologically wide distribution within the different vegetation types mapped by Keay (1959). The most widely distributed subspecies, *O. plenus plenus*, is found in NE. Tanzania in open *Acacia* savannah with a grass cover dominated by *Themeda triandra* (Ratray, 1960). To the south, the *Brachystegia* woodland belt and rift valley separate this population from the main population of the subspecies which forms a continuous belt across the drier 'Mopane' wooded savannah from SW. Angola to Mozambique and the steppe country of Botswana with a grass cover dominated by *Eragrostis*. Evidently the openness of the vegetation and the rainfall regime are of greater importance in delimiting the range of this subspecies than is the species composition of the

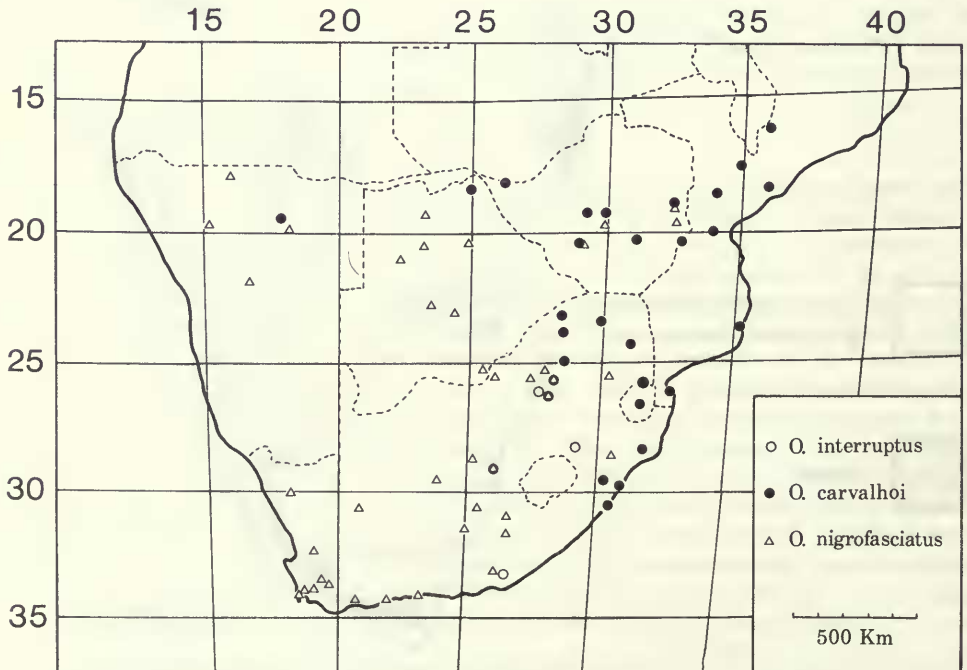


Fig. 152 Distribution of *Oedaleus* species in southern Africa.

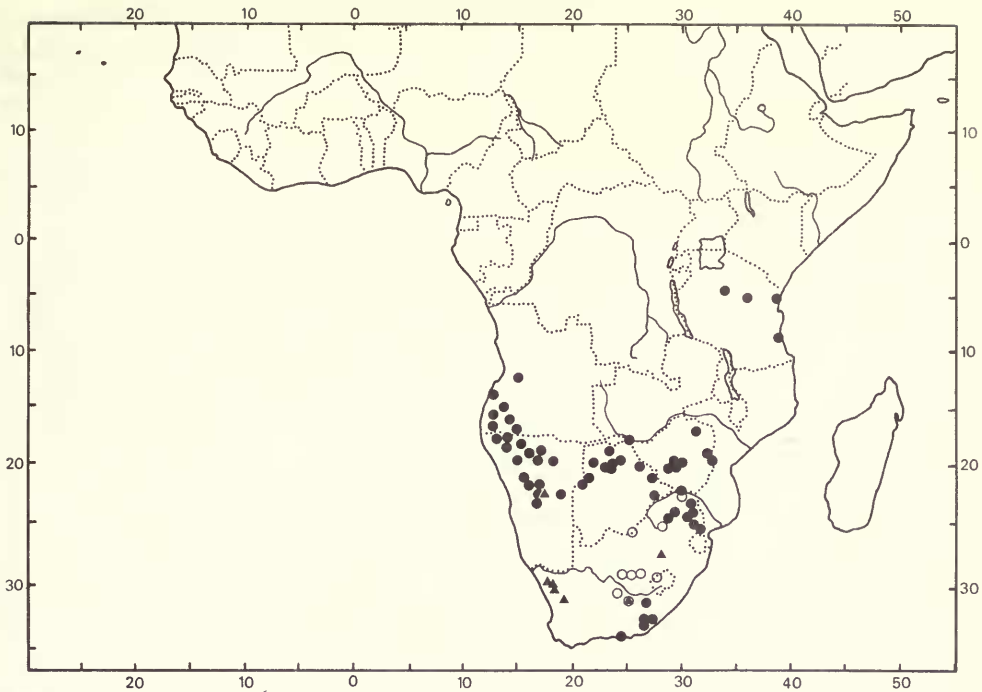


Fig. 153 Distribution of subspecies of *Oedaleus plenus* in southern Africa. Closed triangles, *O. p. plenus*, thin-lined form; closed circles, *O. p. plenus*, thick-lined form; open circles, *O. p. browni*.

grasslands which is quite different in the northern and southern savannahs. Further south there are two distinct populations. One of these, *O. plenus browni*, distinguished by the partial or total absence of the hind wing fascia, is apparently almost restricted to the montane grassland areas dominated by *Themeda* species, which are also the habitat of *O. interruptus*, although it does penetrate into areas dominated by *Hyparrhenia* species to the north and by *Eragrostis* species to the west on lower ground. Rattray (1960) quotes the view of an earlier worker, Acocks, who considered that these areas were also originally dominated by *Themeda* species which have been selectively removed by overgrazing. The montane habitat of this subspecies is entirely contained within that of *O. plenus plenus* which reaches the south coast around Port Elizabeth. Further west, in southern Cape Province an isolated population of *O. plenus plenus* has become adapted to the very distinct winter rainfall area of the western Karroo of Namaqualand. The seasonality of rainfall distribution in South Africa is shown in Fig. 154 (after Adamson, 1938). The figures represent the percentage of the total rainfall falling in the southern summer (October to March). The unusual climate of the region supports a complex plant community with many succulents and a large proportion of endemic genera, including the dominant grass *Ehrharta calycina*. It is probable that the tendency of specimens from this population to have finer pronotal markings is indicative of evolutionary divergence resulting from relative geographical isolation and partial asynchrony of the breeding season caused by the rainfall regime.

*O. flavus*, like *O. plenus*, occurs to north and south of the *Brachystegia* belt (Fig. 155), but the northern population extends northwards across the Equator into Kenya and Somalia whereas *O. plenus* apparently does not. Also unlike *O. plenus*, *O. flavus* occurs as one subspecies, *somaliensis*, in the northern *Acacia* savannah zone, and as another subspecies, *flavus*, in the south where it occupies a habitat similar to that of *O. nigrofasciatus*, even penetrating into the *Macchia* vegetation of the southern Cape. Evidently this is yet another example of colonization across the 'Miombo' woodland during a dry period, with subsequent isolation and divergence. The direction of the migration is assumed to be north to south in view of the greater richness of the *Oedaleus* fauna of

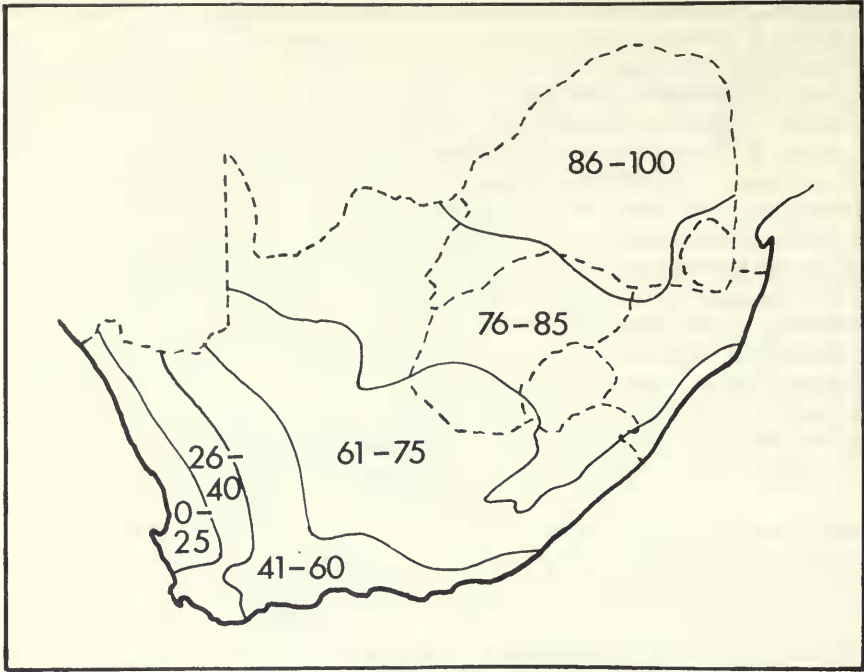


Fig. 154 Map of South Africa showing the percentage of total precipitation falling during the southern summer (October–March) (after Adamson, 1938).

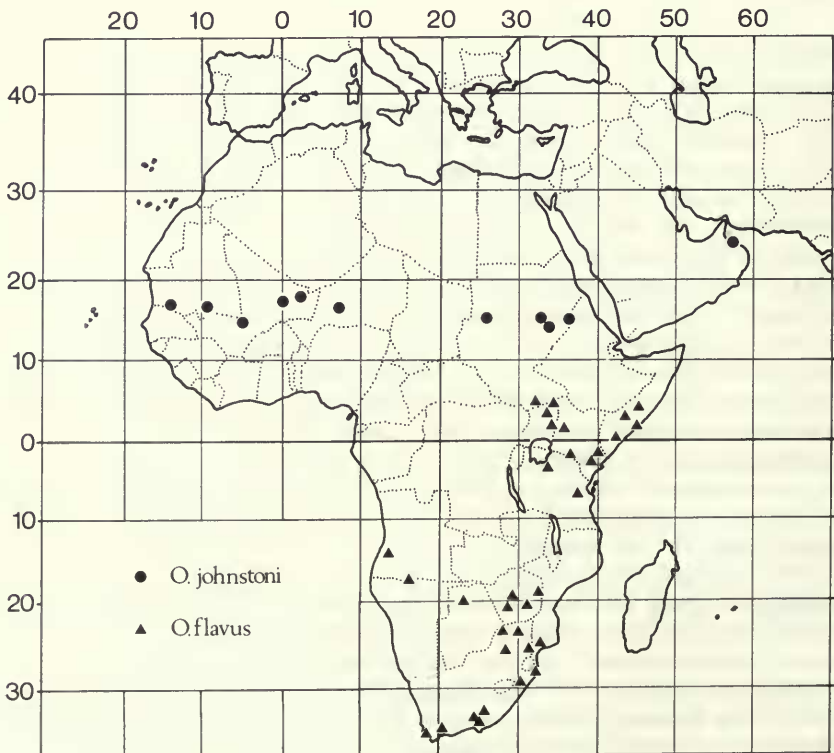


Fig. 155 Distribution of *Oedaleus* species in Africa.

East Africa. The simplest model is that of an East African focus with emigrants travelling south into an area where intrageneric competition would initially be less intense since fewer niches would be filled. However, it is possible that in some instances movement could have occurred in the reverse direction.

### The *Oedaleus* fauna of the Somali peninsula

The most remarkable zone of speciation in *Oedaleus* has been the Somali peninsula. The arid horn of Africa is effectively separated from the latitudinal vegetation belts to the west by the Ethiopian highlands and Lake Turkana. Moreau (1966) lists the area as having more endemic birds than any other lowland non-forest zone in Africa. However, Winterbottom (1967) asserts that the South West Arid District has in fact much the larger avifauna, although direct comparison is impossible. Chapin (1923) considered the area as a distinct avifaunal district (the Somali Arid District) and Popov (1959) found this division relevant to the distribution of the aberrant endemic grasshopper genus *Sauracris* Burr. Both in *Sauracris* and *Oedaleus* it is noticeable that the maximum concentration of species occurs in the northern rangelands. This may in part be due to the wide diversity of structure, vegetation, and rainfall which are experienced within a relatively small area. The climatic zones of the Somali peninsula are shown in Fig. 156 (Griffiths, 1972). Zone I, the northern coastal strip, is characterized by winter rains and summer drought, though high humidity is maintained by land-sea breeze circulation. Zone II, further west, is little studied in terms of its acridid fauna. It is a summer rainfall area, barely reached by the Intertropical Convergence Zone at its most northerly extension, and very hot and arid. Zone III, south of Zones I and II, which constitutes the main portion of the northern rangelands, has a double rainfall peak in spring and autumn but there is great variability both between stations and from year to year (50–750 mm/yr). In this zone the lowest temperatures are reached in winter (December, January). Hemming (1966) and others have drawn attention to the degradation of this area by overgrazing in recent years. Despite this, however, Griffiths (1972) rejects the theory that the overall rainfall has declined during the last century. Further south, Zone IV, covering SE. Somalia and the SE. border of Ethiopia and NE. Kenya, also has a double peaked rainfall but experiences lowest temperatures in summer (July–August). Zone V consists of a SE. coastal strip with high rainfall affected by the Indian monsoon.

*O. nadiæ* is restricted to Zone III, but its known distribution when superimposed on Hemming's Vegetation Map of Somalia (1966) does not suggest any strong habitat preference except for an apparent avoidance of the montane *Juniperus* forest, as would be expected. The floristic diversity of the six localities from which this species is recorded suggests that the major limitation of its range may be a preference for a winter temperature minimum rather than a summer one.

In all, four species of *Oedaleus* are endemic to the Somali peninsula, including *O. inornatus* (Fig. 156), a species with a similar range to *O. instillatus*, and three more extend westwards across the subsaharan latitudinal belt as well, and one species, *O. flavus*, discussed above, occurs as a separate subspecies in southern Africa. This preponderance of species, coupled with a complete lack of West African endemics and the fact that most of the southern African species are closely related, suggests that the Somali peninsula has been the focus of speciation and radiation in the genus. Three members of Group I, one member of Group II, both of Group III, and the two ungrouped species all occur within this area. The species of group II have spread widely. *O. instillatus* is an East African endemic (Fig. 156), but *O. obtusangulus* (Fig. 156) occurs on the far side of the Red Sea in southern Arabia and has a smaller separate population in the mountainous region of Air in northern Niger. The remaining member of the group, *O. roscens*, discussed below, is endemic to the Indo-Pakistan border area (Fig. 157).

### The *Oedaleus* fauna of the subsaharan latitudinal belt

In his reviews of the Pleistocene in Africa, Moreau (1963; 1966) has shown that the Sahara has undergone far-reaching changes during the last 30 000 years. Plant and animal remains from the Ahaggar Massif 400 miles into the western Sahara indicate that Palaeartic elements were able to reach the centre of the desert during cool periods around 20 000–30 000 years ago, and even more recently Mediterranean vegetation apparently reached Air and Tibesti and possibly even further south. Ethiopian fauna also spread across the Sahara to North Africa during the late Pleistocene.



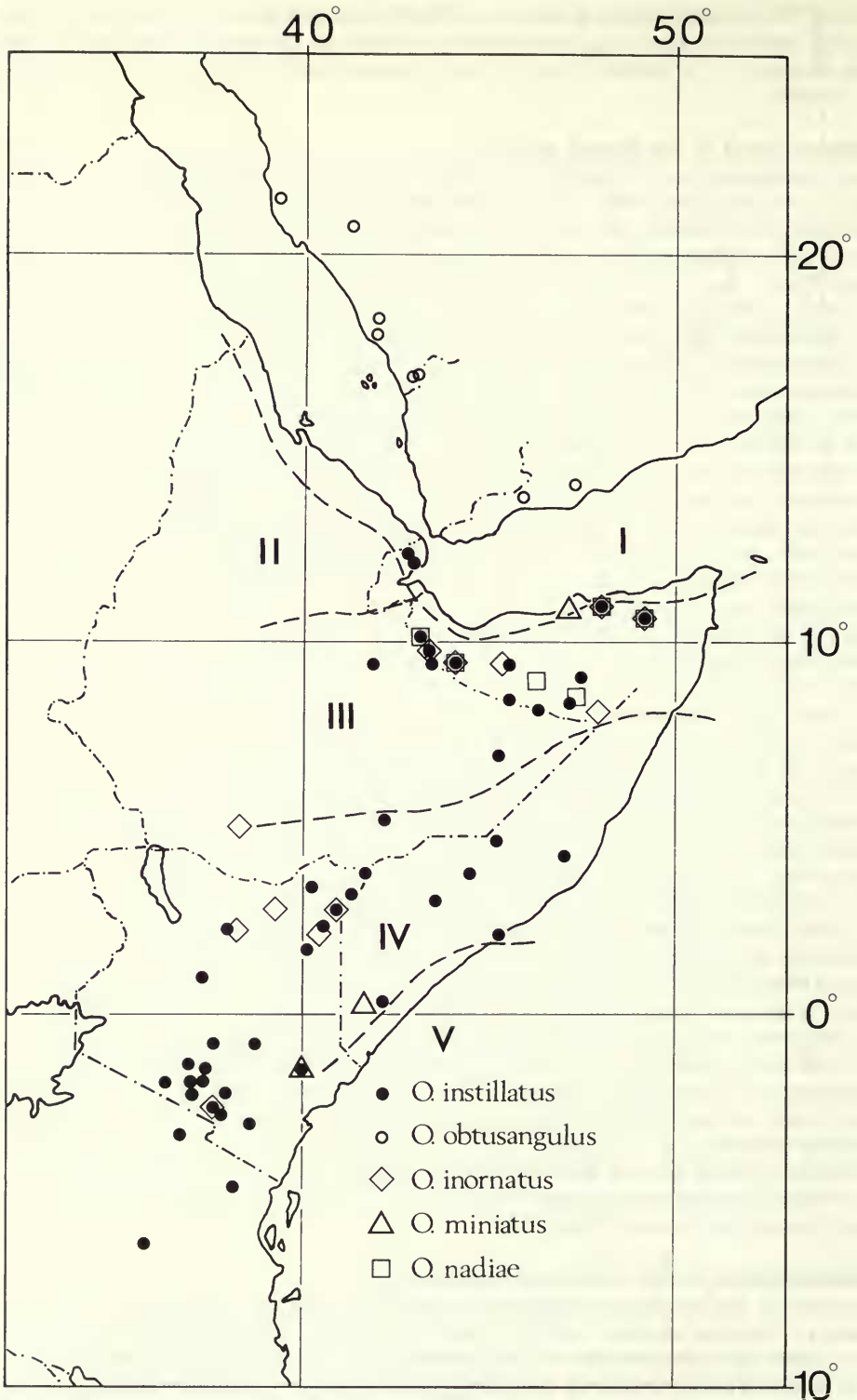


Fig. 156 Distribution of *Oedaleus* species in eastern Africa and south-western Arabia. Dashed lines with Roman numerals, climatic zones (Griffiths, 1972).

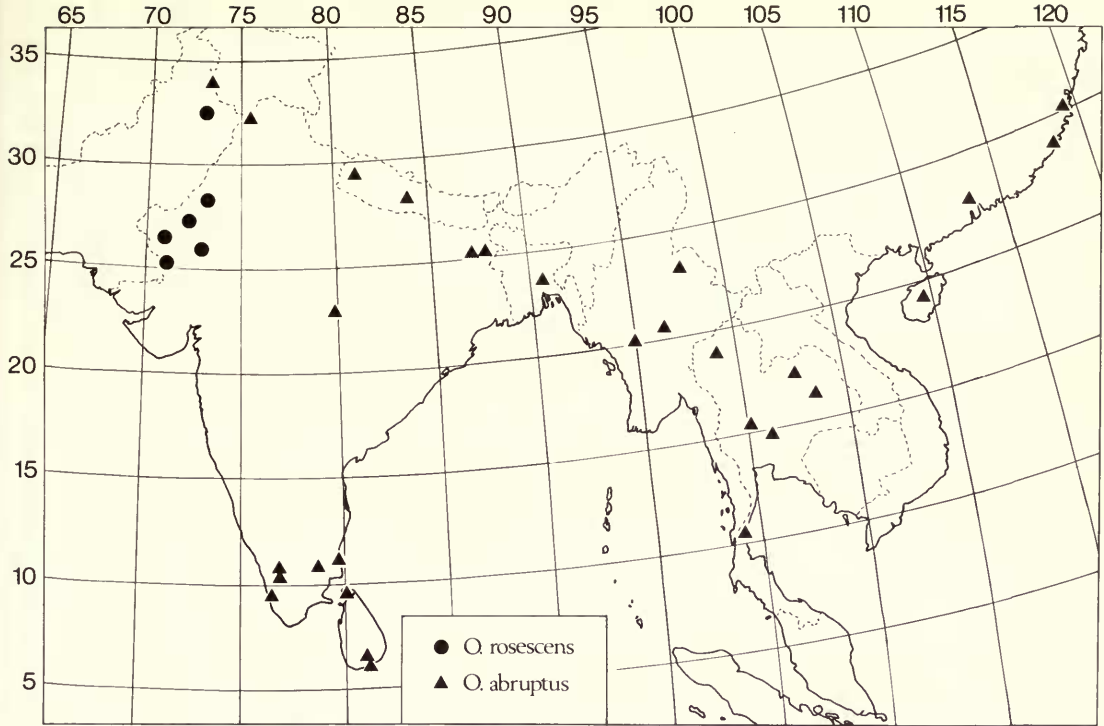


Fig. 157 Distribution of *Oedaleus* species in Asia.

From this Moreau concludes that at least in the western half of the Sahara there was during a period up until about 5000 B.P. no effective barrier to movement. From about that time Tibesti developed an Ethiopian flora, partly as a result of the great enlargement of Lake Chad between about 22 000 and 8500 years ago when it extended for 400 miles north of its present limit and was as large as the Caspian Sea. East of Air, at Adrar Bous, there existed about 8000 years ago a small lake in an area which is now sand desert. To the west of Air, Wadi Azouak, now a dry watercourse, was flowing around 5000 years ago, and, further west still, between Taoudeni and Timbuctoo, an inland basin fed by the upper Niger was forming a large lake (L. Arouane) which broke its eastward sill and drained into the lower Niger around 10 000 years ago. From this it may be seen that the western Sahara enjoyed a period of widespread climatic amelioration.

Van Zinderen Bakker (1969*b*), reviewing recent work on the Pleistocene and Holocene lake levels of the Sahara, indicates that their relationship to rainfall and temperature is very complex and warns against premature attempts to correlate all the available information into a simplistic model. He summarizes available dates for lake deposits into two groups between about 40 000 and 20 000 B.P. and between 12 000 and 3000 B.P. The earlier period is taken as indicative of the effect of the last glaciation which produced a southward movement of the Mediterranean rain belt and reduced the evaporation rate. The second period is coeval with the period of climatic amelioration after the glaciation which may have allowed the penetration of tropical rain from the south. However, the effect of the worldwide brief cold spell at around 5000 B.P. would have been to cause the tropical rain belt to move southwards again and the succeeding higher temperatures would have completed the desiccation which we see today.

These periods of climatic amelioration in the western Sahara during the last 40 000 years would have allowed the three species of *Oedaleus* which today have a subsaharan distribution to move northwards into areas which are now completely inhospitable. This may explain the presence of small populations of *O. senegalensis* in North Africa. *O. decorus*, the only other species of *Oedaleus* which occurs north of the Sahara today, is also a member of Group I and has become

adapted to the winter rainfall Mediterranean zone (Fig. 158). If it originated in Africa south of the Sahara it is impossible to establish positively whether it entered Europe via the Middle East or from North Africa. The present discontinuous distribution of *O. obtusangulus* in SW. Arabia and Yemen and the Air mountains of Niger presumably represents a relic of a much wider continuous distribution during a time of climatic amelioration in the Sahara. This kind of disjunct distribution also occurs in *Truxalis longicornis* (Krauss), but it is surprising that Air should be the only known locality for *O. obtusangulus* in the Sahara since it only just reaches the lower altitudinal limit of montane conditions, whereas Tibesti and Ennedi, or even Ahaggar to the north, are much more substantial mountain refuges. It seems likely that the absence of *O. obtusangulus* from these areas is more apparent than real and that further populations will come to light. The lack of any discernible differences in morphology between the West African and Arabian populations indicates that this is a very recent disjunction.

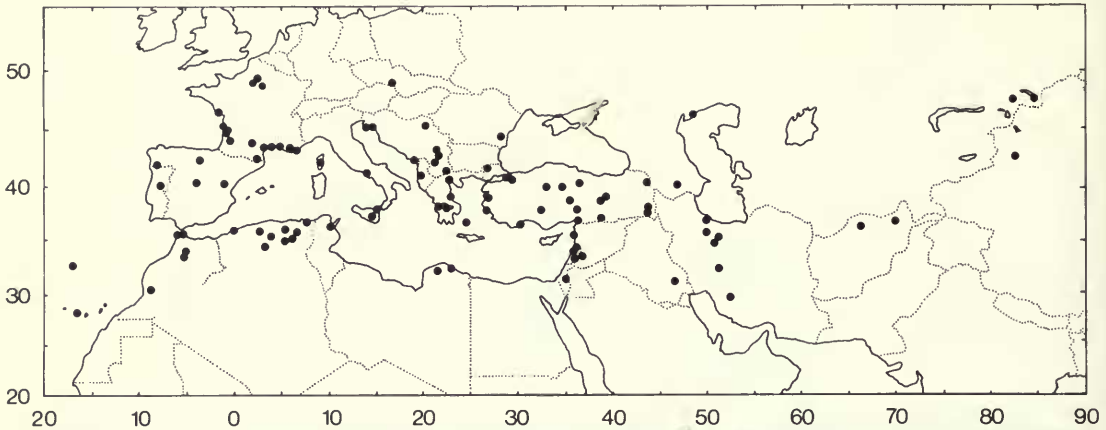


Fig. 158 Distribution of *Oedaleus decorus decorus* in north Africa, southern Europe, and western Asia.

While conditions in the Sahara itself were improved during the periods described above, paradoxically desert conditions moved southwards leaving a line of dead dunes 300 miles south of the present limit of moving sand (Fig. 159). It is known that this would have occurred around 20 000 B.P. at the height of the last glaciation, when the Mediterranean rainbelt moved towards the Equator (Hamilton, 1976). As a corollary of this advance of the desert, all the vegetation zones to the south must have shifted a corresponding distance and the forest would have been reduced to isolated patches.

These dramatic fluctuations of climatic conditions south of the Sahara doubtless account for the poor representation of grassland acridid species, including *Oedaleus*, when compared with eastern and southern Africa. The parallel arrangement of vegetation types from Senegal to Ethiopia has given rise to a corresponding distribution of *Oedaleus* species, of which the most northerly is *O. johnstoni*. This species is sporadically distributed across the subdesert steppe and Sahel savannah (Fig. 155) on silt and clay soils in wadis and on clay plains. In view of the mobility of the species, the unconfirmed record from Oman seems quite credible.

Further south (Fig. 160) *O. senegalensis* forms a broader, overlapping band across the Sahel and into the Somali peninsula. West of L. Chad the southern limit of this species corresponds closely with the belt of dead sand dunes mentioned above (Fig. 159). Isolated populations of *O. senegalensis* exist on both the Canary Is. and the Cape Verde Is. The Cape Verde population has given rise to a melanic form which is described and discussed elsewhere (Ritchie, 1978a). It is, however, of interest that according to Moreau (1966) the present day aridity of the islands has been exacerbated by human degradation of the original endemic vegetation since the discovery of the islands around AD 1460. This has now been reduced to inaccessible patches on cliff ledges. *O. senegalensis* may thus be a relatively recent invader though the eastern islands which are low and

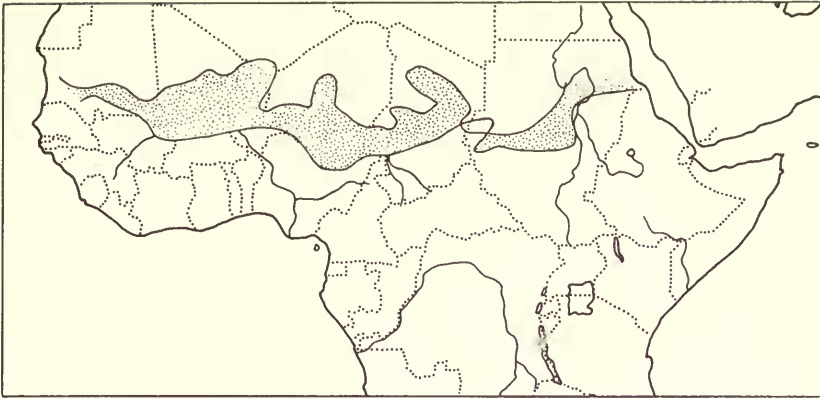


Fig. 159 The evidence for the southward advance of the Sahara during the late Pleistocene (after Hamilton, 1976). Stippled area, belt of fixed dunes.

sandy have probably always been more suitable for the species than the rocky western islands. Outside Africa *O. senegalensis* occurs around the fringes of the Arabian desert and northwards into the western U.S.S.R. and eastwards through Iran to India. An attempt has been made (Batten, 1969) to relate its distribution to the area between the mean annual isohyets of 10 and 40 inches. However, *O. senegalensis* is found in Arabia where the rainfall is less than 10 inches, and in India where it is in excess of 40 inches per annum.

The southernmost subsaharan range is that of *O. nigeriensis* (Fig. 161) which occupies a variety of vegetation types from the Sahel savannah through the *Isobertinia* wooded savannah to the forest-savannah mosaic (Keay, 1959). In East Africa the species occurs in the moist woodland and savannah, particularly in Uganda, and south of the Equator it is found throughout the *Brachystegia* woodland, penetrating as far as southern Zambia. At this point, around 15°S, the mopane wooded savannah recommences and *O. nigeriensis* is replaced by *O. carvalhoi*.

#### The non-african *Oedaleus* fauna

The species of *Oedaleus* found outside Africa are, as stated earlier, either identical with, or closely related on morphological grounds to those of Africa. Madagascar possesses one very widespread endemic species, *O. virgula* (Fig. 162), of which there is one old specimen labelled as from Zanzibar. This record is remarkable if it is genuine since the two islands are well separated and *O. virgula* is not known from Grand Comoro which lies between. Instead *O. nigeriensis* occurs on this island but not on Zanzibar which is much closer to the mainland of Africa and was only separated from it around 10 000 years ago (Moreau, 1966). There is one other old specimen of *O. virgula* labelled as from the Cape, but this can almost certainly be attributed to mislabelling. Very recently Dr N. Waloff has discovered this species on the island of Aldabra, indistinguishable from the Madagascar population. It may well occur on other islands also.

In mainland Asia there are four endemic species of *Oedaleus*. *O. rosescens*, a member of Group II mentioned above, was previously known only from the desert area of NW. Rajasthan and the Salt Range of NE. Pakistan, on the border of another desert area, but it has recently been collected west of the mouths of the Indus at Landhi, near Karachi (Fig. 157). The habitat of this species is probably similar to that of *O. instillatus*, a related species in East Africa, though possibly more arid. Further east *O. abruptus* (Fig. 157), a small species in Group I, has a wide range in the tropical grasslands of southern Asia in lowland areas south of the Himalayas. This species was recently introduced into the island of Oahu in the Hawaiian Is., presumably on United States aircraft returning from SE. Asia to Hickam Air Force Base, Honolulu (U.S.D.A., 1968). Despite eradication attempts the species has now spread to Kauai island more than 100 miles to the west (U.S.D.A., 1976). To the east of the Himalayas *O. infernalis* occurs widely (Fig. 163) in southern and eastern China and into Korea and the extreme south-east tip of the U.S.S.R., in areas with an annual rainfall of between 20 and 60





Fig. 160 Distribution of *Oedaleus senegalensis* in Africa and western Asia.

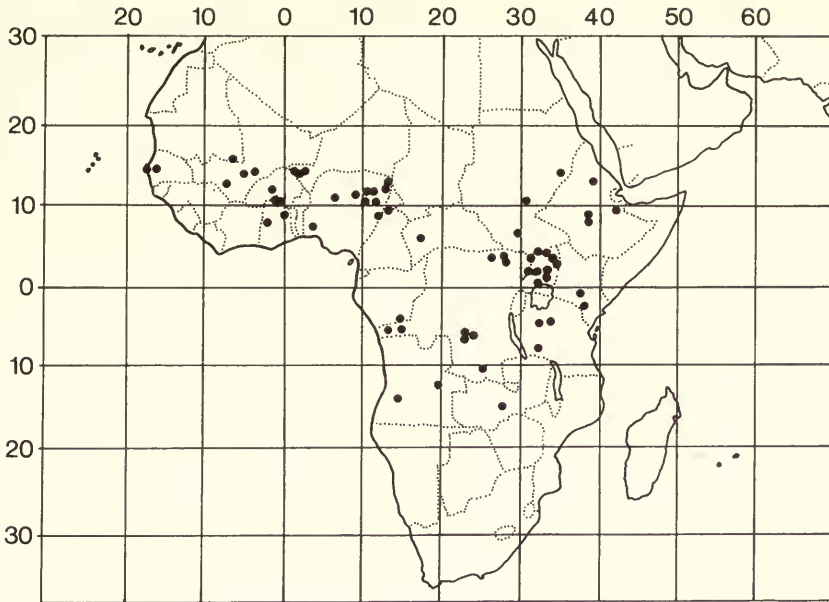


Fig. 161 Distribution of *Oedaleus nigeriensis* in Africa.

inches. This species also occurs in the southern half of Japan, but in Taiwan it is replaced by *O. formosanus*, a little-known related species which appears to be restricted to montane areas (Fig. 163). North of the Himalayas *O. decorus asiaticus* (Fig. 163) is distributed in the western Sayan Range and the Transbaikal region of the southern U.S.S.R., and in Mongolia, with a south-eastward extension into Hopenh and Shantung provinces of China. Much of the range of this subspecies is montane and winter conditions, particularly at higher latitudes, must be very severe.

The furthest point reached by *Oedaleus* is the continent of Australia where one species, *O. australis*, occurs widely in the eastern half of the continent (Fig. 164), apparently independent of vegetation type or altitude but correlated to some extent with areas having an annual rainfall in excess of 10 inches. In the Northern Territory it is probable that the species extends further west than is known at present, but the human population density is low and the area is less well collected than the eastern half of the continent. The absence of *O. australis* from the south-western corner of Western Australia suggests that the species has arrived since the height of the last glaciation when there was a corridor along the south coast between the desert and the sea, formed by the fall in sea level which took place in the Great Australian Bight. This is known to have provided a means of access for non-desert animals to reach the area at that time which have since evolved in isolation from the populations to the east of the desert (W. Bailey, pers. comm.). The single record of *O. australis* from Port Moresby, New Guinea, is a possible indication of the route by which *O. australis* may have reached Australia. However, Key (pers. comm.) suggests that this may be a recent introduction. Parts of the south coast of New Guinea are quite dry but at present no other suitable sites for *O. australis* exist. Presumably New Guinea and the Indonesian Archipelago must have been the bridge by which *Oedaleus* reached Australia, but this could only have been possible at a time when these islands experienced a much drier climate than at present. Whyte (1968) brings forward the lowering of sea level at glacial maxima and the consequent increase of land surface as a possible desiccating factor. However, the decline in precipitation occasioned by the glaciation itself seems a more probable cause of the spread of drought-adapted biota through areas like Malaya, Sumatra, Borneo, and New Guinea which are today mainly covered by rain forest. According to Whyte south New Guinea and Australia have many xerophytic plants which are identical to those of mainland Asia and their immigration is therefore believed to be recent. An alternative but less

likely explanation of the presence of *O. australis* on the far side of a barrier of humid forest would be that it evolved from a form which was initially tolerant of high humidity but became more xerophilous after invading Australia. However, against this suggestion stands the complete absence of any species of *Oedaleus* anywhere between Thailand and New Guinea today. Instead this region has been the setting for a minor radiation of *Gastrimargus* species, a group which throughout its range is consistently more tolerant of humid habitats than *Oedaleus*.

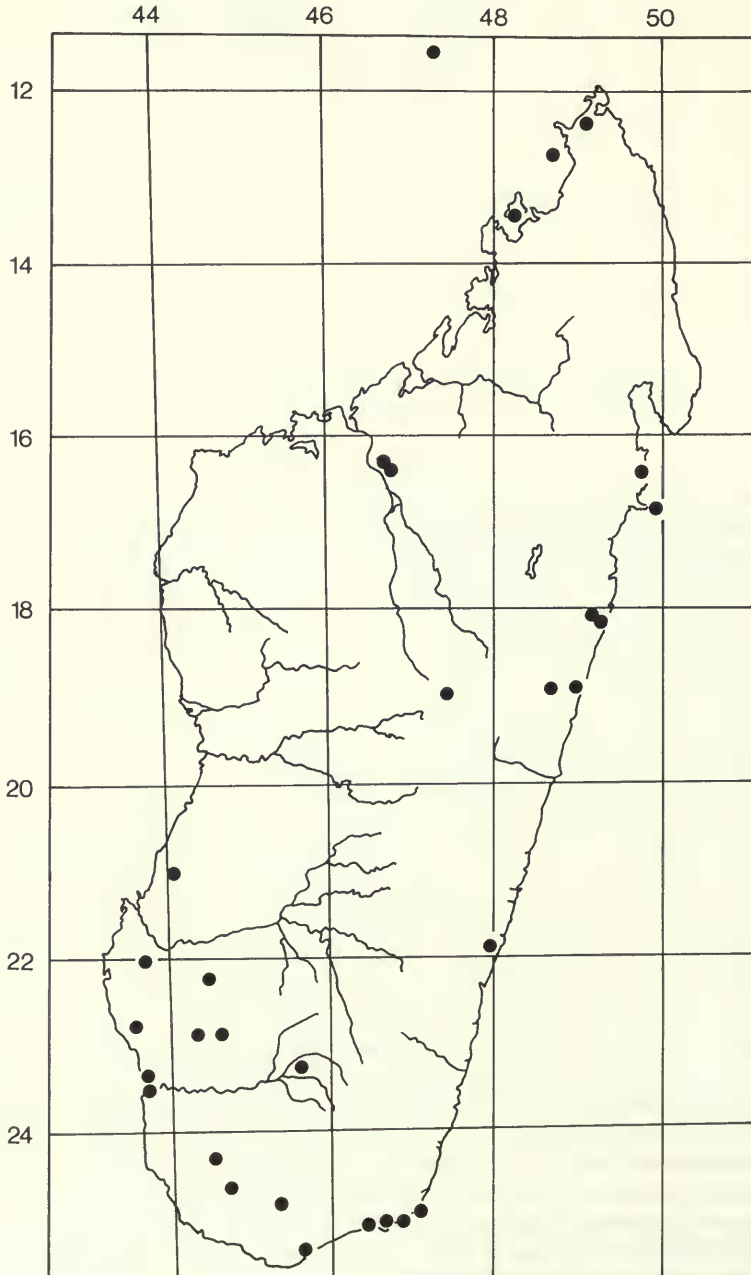


Fig. 162 Distribution of *Oedaleus virgula* in Madagascar.

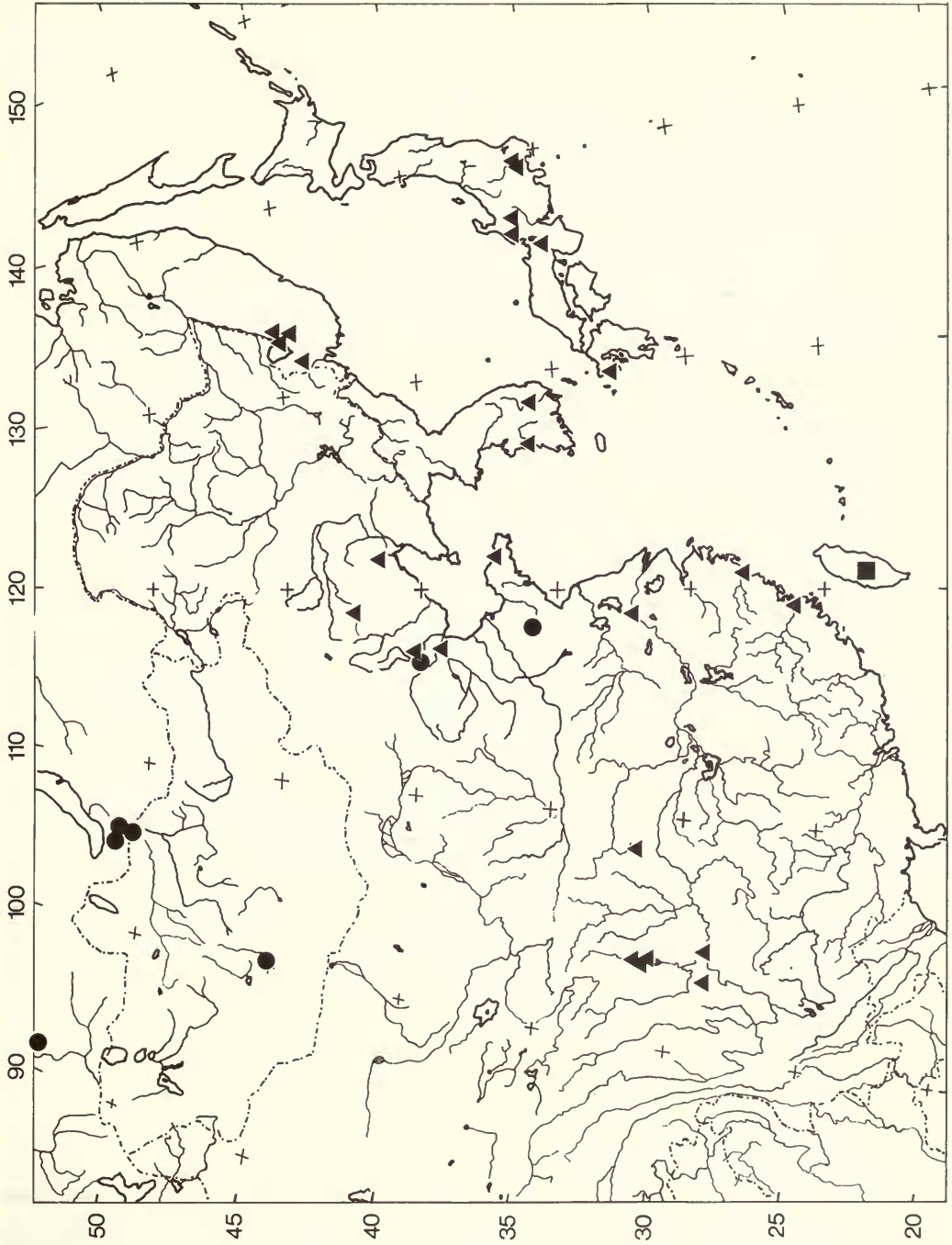


Fig. 163 Distribution of *Oedaleus* species in eastern Asia. Circles, *O. decorus asiaticus*; triangles, *O. infernalis*; squares, *O. formosanus*.



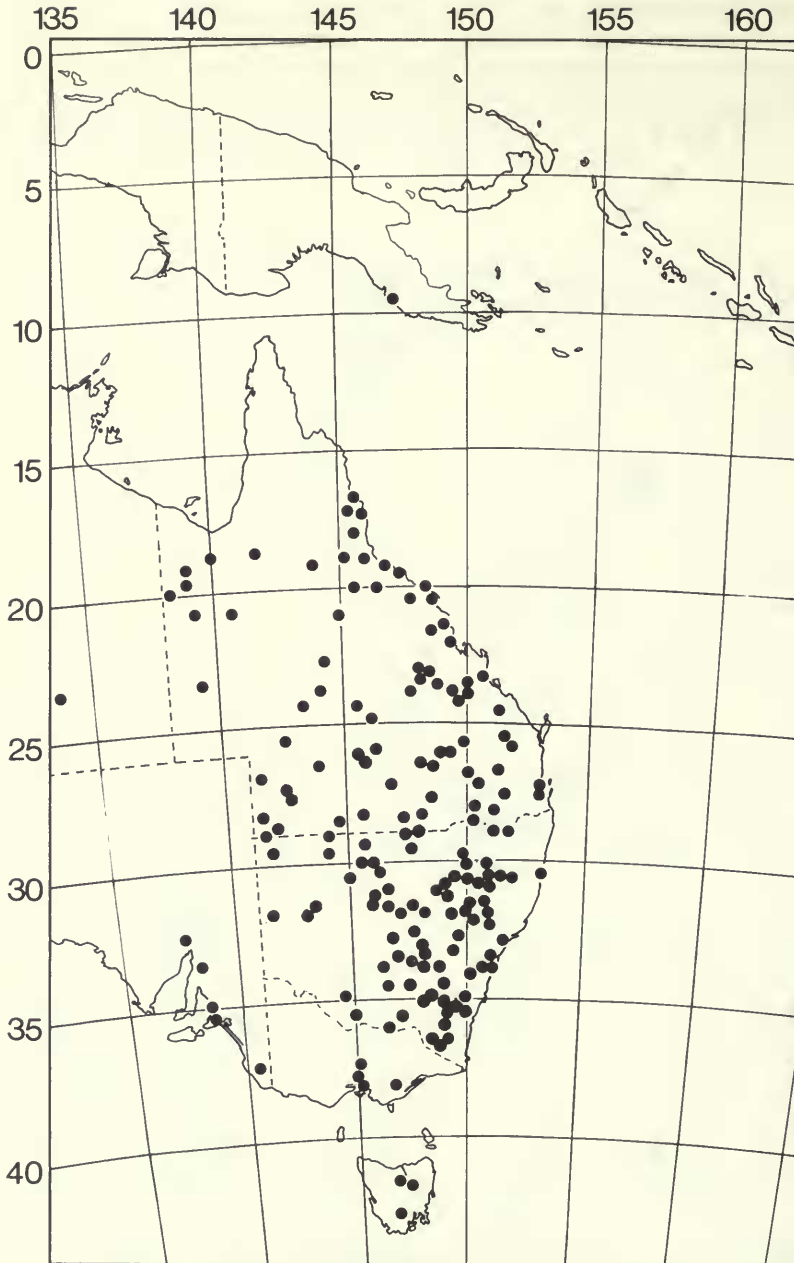


Fig. 164 Distribution of *Oedaleus australis* in Australasia.

#### Problems of analysis of distribution patterns

In discussing the distribution of a large (by the standards of the Acridoidea) genus of mobile savannah grasshoppers there are several difficulties. Firstly, there are relatively few other large genera with similar ecology which have recently undergone revision. La Greca (1970) has shown how ideas of the distribution of the Mantodea have been radically altered after comprehensive revision of the taxonomy of the group. Secondly many species of acridids are of rather infrequent occurrence despite wide ranges, and thirdly many distribution maps are based upon an inadequate coverage of the areas treated simply because collections have not been made. Representation of the

genus *Oedaleus* in collections is probably above average because of the tendency to high population levels in many species and their concentration in the marginal agricultural areas of the Old World tropics and subtropics where locust control organizations have worked extensively.

#### East African acridid diversity

In the above analysis, it has been inferred (p. 159) that *Oedaleus* is of East African origin, and that this is an outcome of the relative climatic stability of the area during the Pleistocene, its partial isolation both then and now, and its present ecological diversity. This is a familiar pattern of distribution since there are at least 114 genera of African grasshoppers which have some representation in East Africa. Of these 42 are endemic to the area, and 26 of those are monotypic genera. This is a very conservative estimate based on Johnston (1956; 1968) without including genera known from Tanzania unless they are also recorded from further north. Genera known from the islands off the coast of Africa are also excluded in the same way. No attempt has been made to supplement Johnston's information from more recent published or museum sources. Such a survey, to be accurate, would require the revision of all the genera of African grasshoppers. For the purposes of this study it may safely be assumed that there are more described genera represented in East Africa than the figures quoted suggest. There are also undescribed genera from Somalia in the BMNH which would swell the list still further.

As indicated above (p. 159), the *Oedaleus* fauna of West Africa is much poorer than that of East Africa and entirely lacks endemic species. This is a reflection of the comparatively rather low degree of endemism among subsaharan savannah grasshoppers in general. It is, however, surprising that although *O. senegalensis* is found on both sides of the Ethiopian Highlands *O. instillatus* only occurs to the east although it is a widely distributed, mobile, xerophilous species. Quite possibly the rather more uniform topography and vegetation of the subsaharan latitudinal zones do not offer sufficient habitats for more than the three which are found there. In addition, despite the fluctuations of climate already mentioned, the mountains of Ethiopia and the deserts on the Eritraean coast and around Lake Turkana (L. Rudolph) must have constituted formidable barriers to any westward expansion by the East African biota. Monod (1971) has noted a parallel case of poor subsaharan representation in the genus *Commiphora*, one of the characteristic plants of Key's (1959) category 'wooded steppe with abundant *Acacia* and *Commiphora*'. Compared to a total of about 80 East African species West Africa has only five. Monod also notes the surprising absence of the gnu and the zebra from the West African savannah.

#### The *Brachystegia* woodland and 'trans-equatorial' speciation

It is apparent from the account of the distribution of *Oedaleus* in Africa given above that the genus divides into different subspecies or species to north and south of the Equator. This kind of distribution pattern is very common in acridids and Jago (1973) has formulated a hypothesis to account for it. According to this theory savannah grasshoppers having an adult diapause initiated by decreasing daylength north of the Equator are out of step with those on the southern side because the daylength and rainfall regimes are six months out of phase. Hence speciation can occur since sexually mature adults on either side of the Equator never meet. The hypothesis is based upon the known mechanism of photoperiodic diapause-induction in *Nomadacris* Uvarov and *Anacridium* Uvarov as studied in the laboratory (Norris, 1959; 1965a; 1965b). However, as Tauber & Tauber (1976) have said in their recent review of insect seasonality: '... to establish when reproduction will begin in the field it is generally necessary to know when diapause ends *in nature* [my italics]. However answers to this problem are usually not well substantiated even for species whose diapause has been studied'. Much field and laboratory work has been done with *Nomadacris* from the Rukwa valley, south of the Equator, and a little on material from the Niger flood plain, north of the Equator. In both areas onset of diapause coincides with changing photoperiod (Uvarov, 1977: 305), and theoretically there would be no time overlap in the breeding period to permit interbreeding. However, termination of diapause in *Nomadacris* may well be effected by temperature change or rainfall (Robertson, 1958), and it is possible that a trans-equatorial migrant would be able to synchronize with the resident population at whatever stage was appropriate. In any event the species appears to have a continuous range from Somalia to South

Africa without any discernible morphological hiatus at the Equator so it cannot at present be considered as offering material support to a belief in an 'Equatorial Species Dynamo'.

Another factor which tends to weaken the general applicability of a specifically trans-equatorial mechanism is the prevalence of egg rather than adult diapause in Acridids. For example, 13 out of the 51 species of Sudanese Acridoidea investigated by Joyce (1952) survive the dry season in the egg stage. In species such as these the initiation of diapause may be in response to changing day length, but this response gradually weakens in preparation for post-diapause development (Tauber & Tauber, 1976), and once again the actual trigger for development to recommence may simply be rainfall. In *O. senegalensis* in India there is evidence that rainfall between six months and one year after laying is sufficient to break diapause (Venkatesh *et al.*, 1971). The occurrence of intercalary hatching in December, 1961 in the Cape Verde Is., in response to unusually heavy rain (Saraiva, 1962; Batten, 1969), may indicate that eggs can hatch soon after laying, even at the end of the season when they would normally diapause. Clearly, if photoperiod does influence egg diapause in *O. senegalensis*, the influence is on its induction and may be weak and of short duration. A trans-equatorial migrant of this species would presumably have no difficulty in adjusting to the new seasonal timing.

Jago (1973) has pointed out that *Locusta* in Africa cannot exist at high population densities after invading areas south of the Equator. However, this species appears unable to maintain high densities anywhere else either, apart from the main outbreak area in the flood plain of the Niger. There are in fact many species which do succeed in spanning the Equator apparently without alteration (e.g. *Dnopherula cruciata* (Bolivar), *Humbe tenuicornis* (Schaum), *Trilophidia conturbata* (Walker)) though there is always the possibility of unrecognized cryptic speciation. The most well-studied example of this phenomenon concerns *Eyprepocnemis plorans* (Charpentier). This species was divided by Dirsh (1958) into several 'subspecies' of which *E. p. ornatipes* (Walker) and *E. p. meridionalis* Uvarov are found to the north and south of the Equator respectively. John & Lewis (1965) demonstrated meiotic breakdown in hybrids between these 'subspecies', indicating that speciation had occurred. No F<sub>2</sub> generation hybrids could be produced. There is, however, no direct evidence that this was directly attributable to trans-equatorial effects. *E. p. ornatipes* is apparently not found nearer to the Equator than northern Kenya, while *E. p. meridionalis* in the south penetrates northwards as far as 3°S on the west but only about 7°S in the east of Tanzania. Remarkably, the intervening area is occupied by a hybrid not between these two species or subspecies, but between *E. p. meridionalis* and *E. p. plorans*, the Mediterranean form. Clearly this is a rather complex situation, but one feature of it, the diagonal northern boundary of the *E. p. meridionalis* zone just south of the Equator in N. Tanzania, recurs time and time again in the distribution of African acridids and is particularly noticeable in *Oedaleus*. Examples of northern species which show a discontinuity at this point are *O. senegalensis*, *O. flavus somaliensis*, *O. instillatus*. All these cross the Equator but are apparently unable to advance across the *Brachystegia* woodland zone, within which the only species of *Oedaleus* found is *O. nigeriensis*.

In *Aiolopus simulatrix* (Walker), a member of a related genus revised by Hollis (1968), there is a good example of subspeciation exactly at the northern boundary between the savannah and woodland. On the savannah side of the boundary occurs *A. simulatrix simulatrix*, and on the woodland side to the south is found *A. s. femoralis* Uvarov. Some acridid species, including *O. plenus plenus* and *Aiolopus meruensis* Sjöstedt, occur both north and south of the barrier apparently unaltered, but are never found within the woodland itself. Other species are split into subspecies or species pairs either at the savannah/woodland boundary or across the width of the woodland barrier itself. The major examples of these effects have been described above. Key (1959) has pointed out the importance for grasshoppers of 'ecotones and mosaic habitats in which the scale of the patchwork is adjusted to the vagility of the species'. In *Acorypha* Krauss, a genus of grasshoppers of rather low vagility, speciation has occurred in response to quite small scale geographical features. This has perhaps been assisted by ecological specialization and the variability of genital morphology allowing pre-mating isolation of newly diverged forms. Only in one species, *A. glaucopsis* (Walker), is there a clear separation at the savannah/woodland boundary, regarded by Jago (1973) as a delayed response to the Equator. *Oedaleus* and *Aiolopus* on the other hand are both xerophilous genera of high vagility requiring as a rule wide separation to prevent



continual reinvasion of disjunct populations. This is particularly true in view of the low level of interspecific variation both in ecology and in genital morphology. The suddenness of specific and subspecific discontinuities and the number of species in which they may be observed, are strong evidence in favour of the view that speciation among the more xerophilous savannah grasshoppers occurs not at the Equator but on the northern and southern boundaries of the *Brachystegia* woodland, which constitutes a barrier of no less than 500 miles at its narrowest point, and effectively much wider, particularly when the Southern Highlands of Tanzania are added to the problems encountered by migrant insects.

#### The woodland barrier and the 'arid corridor': evidence from other groups

The evidence for the importance of the *Brachystegia* woodland barrier in the evolution of the Acrididae discussed above is strongly reinforced by recent biogeographical studies of other groups of animals and plants. The affinities between the biota of the arid and semi-arid regions of south-western and north-eastern Africa have been noticed by many biologists and in recent years several of them have suggested that there must have been a former link between the two areas. For example Monod (1971) has shown that of 556 genera of flowering plants occurring in the Sahel 354 (63%) also occur in the southern savannah. Balinsky (1962) has indicated the existence at the present day of an 'arid corridor' joining these regions which could be defined in terms of a rainfall of less than 10 mm per month during at least three consecutive months (Fig. 165). The disjunct distribution patterns of large numbers of plants and animals suggest that, for them at least, the arid corridor is no longer effectively open and that the belt of *Brachystegia* woodland now constitutes a complete barrier between the more arid regions north and south. Monod (1971) found that out of 84 genera of flowering plants analysed 50 had disjunct north/south distributions. Forty species of plants and two species of coprophilous fungi were found to occur in the northern and southern arid zones but nowhere in between, and Lebrun (1971) has described four more cases of flowering plants with the same disjunct range. De Winter (1971) noted that in the Poaceae alone there were 17 species with discontinuous distributions in the northern and southern arid areas.

Discussing the resemblances of the bird fauna of north-east and south-west Africa, Winterbottom (1967) has estimated that there are 205 species in the south-west arid zone and 133 in the former British Somaliland and the Gulf of Aden. Of these about 30 species are held in common either as the same or different subspecies, species pairs, or close relatives. From this analysis Winterbottom reached the following conclusions: 1, the necessity of a past connection between the arid faunal areas of Chapin (Fig. 166); 2, the different degrees of differentiation between northern and southern populations suggest that there has been more than one period when the corridor was open; 3, the high degree of endemism in the two areas suggests that the link between them has been of brief duration or incomplete, or both. He makes the suggestion that the link would have followed the Luangwa valley which at present carries more open vegetation north-eastwards far into the *Brachystegia* zone. Even today several southern bird species penetrate northwards along this valley to within 150 miles of the dry wooded steppe of NE. Tanzania which advances south along the valley of the Great Ruaha river.

Among mammals also there are striking examples of disjunct distribution which suggest the existence of a former connection between the northern and southern arid zones. Roberts (1937a; 1937b) noted the discontinuous ranges of the dik-dik, *Madoqua kirki*, which has a south-western subspecies *damarensis* (Monod, 1971), and of the oryx, which forms a species pair with *Oryx gazella* in the south-west and *O. beisa* in the north-east (Meester, 1965). Meester has also noted further examples including the bat-eared fox, *Otocyon megalotis*, occurring in both arid regions, and the gerbil which has two closely related species in the two areas. Bigalke (1968) has estimated that the Somali peninsula has about 15 endemic mammals and notes the occurrence of a distinct species of hartebeest, *Alcelaphus lichtensteinii*, in the *Brachystegia* zone separating different subspecies of *A. buselaphus* in the north-eastern and south-western arid areas. As further evidence of a past corridor Verdcourt (1969) has stated that fossil material of the genenuk, 'a typical Somali thornbush antelope extending into N. Tanganyika' has been found at Broken Hill in Zambia, an area presently surrounded by *Brachystegia* woodland.





Fig. 165 Distribution in Africa of arid regions having less than 10 mm of rainfall per month during at least three consecutive months (after Balinsky, 1962).

Bigalke (1968) considers the observed overlap of some woodland mammals into arid areas as encroachment. However, they could also be regarded as relicts of former woodland extensions. For example Davis (1962) has noted that several southern African species of Muridae which avoid arid areas reach as far north into the savannah as the Tana river watershed in southern Kenya, a level known to zoogeographers as 'Sclater's Line'. Kingdon (1971) suggests that a past extension of the Congo forest eastwards from the north of L. Victoria to Sclater's Line was responsible for the racial divisions of hartebeeste and savannah monkeys (*Cercopithecus*) to the north-east and south-west. Even under present day conditions one may see from the vegetation map of Africa (Keay, 1959) that there is a considerable barrier to movement of lowland savannah biota across this mosaic of lakes, montane forest, and moist woodland. An additional isolating factor already mentioned above (p. 159) in relation to latitudinal movements, but equally important in impeding north-south mobility, is the desert and subdesert extending south-eastwards from L. Turkana. If it is certain that forest and woodland have on occasions formed an effective barrier under extreme pluvial conditions, it is at least probable that under conditions of increased aridity the Turkana desert would have enlarged sufficiently to impede the migration of less xerophilous biota.



**Fig. 166** Outline map of Africa showing Somali Arid and South West Arid Districts (vertical lines) and the suggested past corridor between them (dots) (after Winterbottom, 1967).

Among entomologists the faunal links between the northern and southern arid zones have apparently received relatively little attention. Koch (1960) has noted the similarities between the Tenebrionid beetle faunas of the Namib desert and the deserts of northern and eastern Africa and even Asia at the tribal level. The extensive and often sympatric speciation in the Namib and the very high degree of specific endemism indicate an ancient union of this area with other deserts in Africa and Asia. However, this could only have resulted from an earlier, more sustained, and more extensive period of aridity than that being postulated here as responsible for the reunion of semi-arid rather than true desert biota. In the Rhopalocera Carcasson (1964) has shown that north-east/south-west speciation is rare since butterflies are essentially insects of forest and woodland which have not extensively colonized the more open vegetation zones. However, there are minor centres of speciation within the *Brachystegia* woodland and in the north-east arid zone. By contrast to the Tenebrionidae, the butterflies have no centre of radiation within the south-west arid zone. There are, however, disjunct north/south distributions in the genera *Dixaea* and *Colotis*. Carcasson

notes that even those species of *Colotis* which are tolerant of woodland have undergone speciation as a result of a past eastward extension of the forest.

This brief review of recent literature indicates a growing awareness of the rôle of the *Brachystegia* woodland barrier in the evolution of the savannahs and steppes of Africa, and the past existence on one or more occasions of an arid corridor between the north-eastern and south-western semiarid zones. In addition to this biogeographical evidence there is a growing body of palaeoecological data to assist in reconstructing the changes in the climate and vegetation of Africa during the late quaternary. A useful summary has been given by Van Zinderen Bakker (1976) whose theoretical reconstruction of the vegetation of subsaharan Africa has been mentioned earlier (p. 154 & Fig. 151). In this review (p. 174) Van Zinderen Bakker concludes that during 'dry glacial times . . . the 'arid corridor' . . . would have been open'. However, in an earlier paper (1969c: 139) he had suggested that 'present-day rainfall maps show that a corridor . . . probably existed during periods with a higher temperature'. He added that pollen analyses at Kalambo Falls at the southern end of L. Tanganyika show that 'conditions could have been hot and dry in the gap between the Ufipa Plateau and the Malawi Mountains during one of the warm interstadials or during the postglacial temperature optimum'. Hamilton (1976) puts the case for the fragmentation of the Congo forest during at least the period of the last glacial maximum between 25 000 and 12 000 B.P. and suggests that the forest may not previously have been continuous across the Congo basin until as far back as 75 000 B.P. During some part of this period the East African arid corridor was presumably open, at least partially or intermittently. In an earlier review of the subject Moreau (1966) had put forward the theory that montane forest would have descended from about 1500 m to 500 m at the last glacial maximum, isolating lowland savannah biota in widely separated refuges, but this has since been rejected as unrealistic (Van Zinderen Bakker, 1975).

### Conclusions

From the above it will be apparent that the exact timing and duration of any past breaches in the woodland barrier, and the degree of contact between north and south that they afforded, are still matters for discussion. What now seems certain, however, is that the *Brachystegia* is an effective isolating mechanism at the present time, and that it has been breached by a corridor of more open vegetation one or more times in the past. The effect this has had on the flora and fauna of Africa is becoming steadily clearer. In the Acridoidea the cyclical separation and reunion of the eastern and southern savannahs explains much of the observed speciation and subspeciation in xerophilic genera. In view of the subtlety of the morphological changes which often accompany this evolutionary process there is a need for thorough revision of savannah genera with more attention to biogeographical considerations. The possibility that cryptic speciation may occur in disjunct populations of acridids highlights the importance of cytogenetic studies like those of John & Lewis (1965) on *Eyprepocnemis plorans* as a necessary back-up to morphological methods. The more precise understanding of the taxonomic status of grasshopper populations which could be gained by such studies would be of practical service in the control of pest species by indicating whether biological data which have been gained, for example, from northern populations of a species are likely to have only limited application to southern populations.

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